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1953—1955

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ERRATA

P. 65, first entry should read: Bohn, G. 1902 .. *Bull. Sci. Fr. Belg.*, **36**: 178–551, *etc.*

P. 265 (title-page): For "2 Plates" read "2 Figures."

THE OSTRACOD GENUS *TRACHYLEBERIS*

J. P. HARDING

AND

P. C. SYLVESTER-BRADLEY

BRITISH MUSEUM
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NATURAL HISTORY

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ZOOLOGY Vol. 2 No. 1
LONDON: 1953

THE OSTRACOD GENUS *TRACHYLEBERIS*

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13 MAR 1953

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Issued February, 1953. *Price Four Shillings.*

THE OSTRACOD GENUS *TRACHYLEBERIS*

By J. P. HARDING AND P. C. SYLVESTER-BRADLEY

SYNOPSIS

When Brady erected the genus *Trachyleberis* for a species which he had described earlier as *Cythere scabrocuneata*, he had before him specimens from New Zealand which did not in fact belong to that species.

Both the type specimens of *Cythere scabrocuneata* and the specimens from New Zealand are in the British Museum (Natural History). A new name is proposed for the New Zealand species and full descriptions of the type specimens of both species are given; fortunately they are congeneric.

BRADY (1880) described the shell of a new species of ostracod, *Cythere scabrocuneata*, from specimens collected by the "Challenger" Expedition. Later he (Brady, 1898) described the limbs and other soft parts of further specimens from Lyttelton Harbour, New Zealand, which he thought belonged to the same species, and as the limbs showed some unusual features, he erected a new genus *Trachyleberis*. Müller (1912) and Skogsberg (1928) considered *Trachyleberis* to be synonymous with *Cythereis* Jones, but, as one of us has shown elsewhere (Sylvester-Bradley, 1948*b*), the shell of *Trachyleberis* differs significantly from that of *Cythereis*, and the genus was therefore revived, though without reference to the soft parts.

Some of the original "Challenger" material is preserved in the British Museum (Nat. Hist.) in the form of dry shells gummed to wooden microscope slides, and the Lyttelton Harbour material, consisting of several specimens of both sexes, is preserved in spirit in the Hancock Museum, Newcastle, and we are much indebted to the Curator, Mr. C. E. Fisher, for letting us examine this material. He has also graciously permitted some of the material to be kept at the British Museum. We also re-examined the "Challenger" specimens and found that some of what Brady refers to as "empty shells" had a few appendages still inside them; and by treating the whole ostracod with a 1% solution of tribasic sodium phosphate (Na_3PO_4) it has been possible to recover these appendages and make permanent mounts.

It is now quite evident that these "Challenger" specimens and the ones from New Zealand are different species, and that the Lyttelton Harbour specimens must be given a new name; we propose to call them *Trachyleberis lytteltonensis*.

It is unfortunate that the only specimens in the British Museum (Nat. Hist.) of the "Challenger" collections are from the Inland Sea of Japan, as Brady describes *C. scabrocuneata* from three different localities, the Bass Straits, the Inland Sea of Japan and Wellington Harbour, New Zealand, and it is quite possible that the Wellington Harbour specimens were the same species as those from Lyttelton Harbour, as both are from New Zealand harbours. Should these two species ever be put into different genera the name *Trachyleberis* will have to remain with the Japanese species, *T. scabrocuneata*, which must be based on the only available type material. This is in spite of the fact that it was characters which Brady saw in the New Zealand specimens, now called *T. lytteltonensis*, which led him to erect his new genus.

The present paper attempts to describe these two species. Although it is intended as a contribution to the taxonomy of the genus, we do not append a formal diagnosis. We feel that as yet too few species are known by the details of both shell and soft parts.

As the specimens from Lyttelton Harbour are more complete they will be described first.

TRACHYLEBERIS Brady, 1898

Type-species (by monotypy) : *Cythere scabrocuneata* Brady, 1880.

Trachyleberis lytteltonensis sp. nov.

(Text-figs. 2–19 ; Pl. 1, figs. 1–4, 7 ; Pl. 2, figs. 1–4, 7, 8)

Trachyleberis scabrocuneata, Brady, 1898, Trans. Zool. Soc. Lond. **14** : 444, pl. 47, figs. 1–7, 18–25.

Trachyleberis scabrocuneata, Hornibrook, 1952, New Zealand Geol. Surv., Palaeont. Bull. **18** : 32–33, pl. 3, figs. 38, 39, 48.

MATERIAL. About 40 specimens preserved in spirit from the Brady collection, Hancock Museum, Newcastle-on-Tyne, dredged at 1–5 fathoms from Lyttelton Harbour, New Zealand. The holotype and other figured specimens have been mounted, and through the generosity of the Hancock Museum are now kept at the British Museum (Nat. Hist.); these bear the following registered numbers: 1952.12.9.1–12.

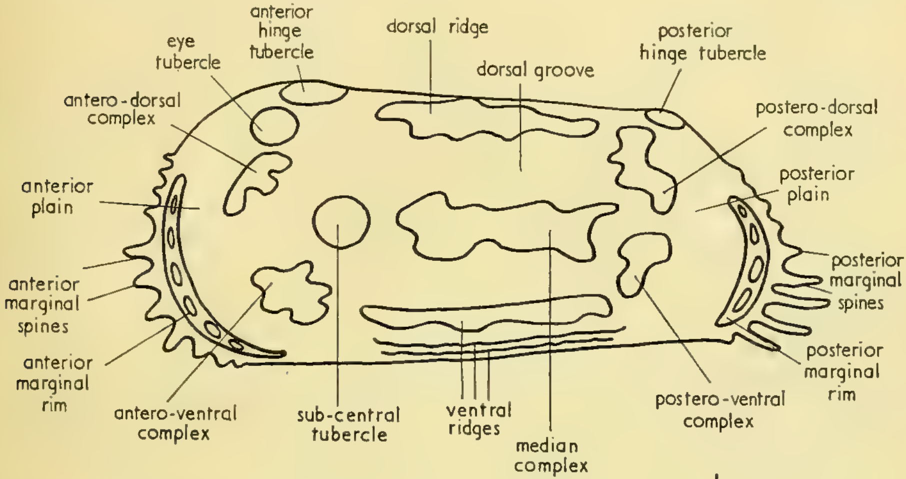
OCCURRENCE. In addition to its occurrence in the type locality *T. lytteltonensis* has been reported by Hornibrook (1952, pp. 69, 71, under the name "*T. scabrocuneata*") from four stations in the seas of the New Zealand area dredged at depths ranging from 28–67 fathoms, and from one fossil locality in the Upper Miocene (Tongaporutuan) of New Zealand.

HOLOTYPE. Male, B.M. 1952.12.9.1.

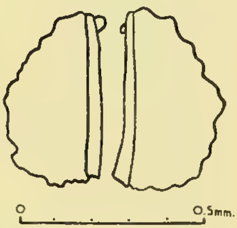
PARATYPES. Both sexes, B.M. 1952.12.9.2–12.

DESCRIPTION. The carapace is subrectangular in lateral outline, with the dorsal and ventral borders nearly straight, and converging but slightly towards the posterior (Pl. 1, figs. 1–4). The anterior border is rounded, the posterior triangular, the postero-dorsal margin being straight or slightly concave, the postero-ventral margin curving evenly into the ventral margin. Sexual dimorphy is strong, the males being longer in proportion than the females (see table below). In dorsal view (Pl. 2, figs. 1–4) the carapace is seen to be widest in the region of the sub-central tubercle, and is compressed in the regions of the anterior and posterior plains. In end view (Text-fig. 2) the carapace appears approximately triangular, both valves showing a fairly abrupt ventral angulation, and the venter being almost flat. The left valve is larger than the right, its selvage fitting outside that of the right throughout its course.

		Length	Height	Width (of complete carapace)
Dimensions :	♂ B.M. 1952.12.9.1 .	1·08 mm.	0·49 mm.	0·49 mm.
	♀ B.M. 1952.12.9.6 .	0·90 ,,	0·49 ,,	0·49 ,,
Proportions :	♂ B.M. 1952.12.9.1 .	2·21	1	1·00
	♀ B.M. 1952.12.9.6 .	1·84	1	1·00


anterior hinge tubercle
eye tubercle
dorsal ridge
posterior hinge tubercle
dorsal groove
antero-dorsal complex
postero-dorsal complex
anterior plain
posterior plain
posterior marginal spines
anterior marginal spines
anterior marginal rim
posterior marginal rim
antero-ventral complex
sub-central tubercle
ventral ridges
median complex
postero-ventral complex

1



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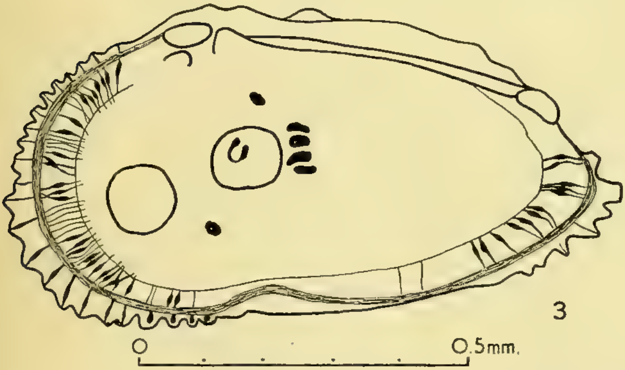


3

Text-fig. 1. Diagram to illustrate the terms used in the description of the external ornament of the carapace in the Trachyleberidae.

Text-fig. 2. *Trachyleberis lytteltonensis* sp. nov. Profile in end view from the posterior. B.M. 1952.12.9.6.

Text-fig. 3. *Trachyleberis lytteltonensis* sp. nov. Internal lateral view of right valve. B.M. 1952.12.9.6.

The following analysis of the ornament (see Pl. 1, figs. 1–4) follows a scheme previously put forward (Sylvester-Bradley, 1948*a*) illustrated by Text-fig. 1. Eye tubercles are prominent on both valves, and run into the antero-dorsal complex, which consists of a simple swelling. The sub-central tubercle forms a prominent mammillated boss, and the antero-ventral complex consists of four tubercles. Behind the sub-central tubercle the ornament is not clearly divided into ridges and complexes, but consists of a number of tubercles, which have a tendency to bear slightly mammillated summits (this character is not well shown by the photographs reproduced in Pl. 1, which are of specimens coated with magnesia). There are three ventral ridges, the uppermost bearing elongated tubercles. The anterior marginal spines are divided into two groups, a dorsal set of smaller rounded spines, and a ventral set of larger more pointed spines. The anterior marginal rim is composed of a double line of tubercular spines, which supplement the armature of the margin. The posterior marginal spines are prominent in the ventral region, but almost absent dorsally. The posterior marginal rim is less well developed than the anterior, and is armed with fewer tubercles. The anterior hinge tubercle lies behind and above the eye tubercle in both valves, and the posterior hinge tubercle of the left valve forms a prominent swelling near the commissure, best seen in dorsal view.

The duplicature is fairly wide, extending 0·05 mm. inwards from the selvage in anterior and postero-ventral regions, and up to 0·07 mm. at the posterior extremity. The selvage is prominent in both valves, and follows a sinuous course along the ventral margin, being markedly concave to the exterior in the centre of the venter. There is no vestibule.

Radial pore canals (Text-fig. 3 ; Pl. 1, fig. 7) run to each marginal spine and to each tubercle of the marginal rim. Some (presumably those serving the marginal spines) terminate along the inner margin ; others (presumably those serving the rim) terminate on the inner surface of the shell just inside the inner margin. The total number of radial pore canals is therefore rather large, and they appear crowded, and sometimes superimposed in lateral view. Most of them are inflated towards the middle. The normal pore canals are few in number, one serving each tubercle of the ornament in the same manner as the radial canals.

The sub-central tubercle appears as a muscle scar pit on the inside of the valve (Text-fig. 3). The muscle scar pattern is that characteristic of so many of the superfamily, with four slightly elongated scars, lying vertically above each other, to the posterior of the pit, and a single scar, U-shaped, opening upwards, within the pit. In addition there are two other scars, one above and one below the main group. Each scar is raised as a tubercle on the inside of the valve.

The antero-ventral complex forms a pit on the inner surface of the valve similar in nature to the muscle-scar pit (Text-fig. 3).

The hinge of the left valve (Pl. 2, figs. 1–4, 7, 8) consists of two terminal slightly elongated sockets, unbounded on the ventral side, and a median element subdivided into an anterior rounded projecting tooth and an adjoining posterior finely crenulated bar. In the right valve the anterior tooth projects beyond a less strongly projecting base. The posterior element is a slightly elongated lip-like tooth. The median element is a groove subdivided as in the left valve to provide a deep anterior socket, open ventrally, behind the anterior tooth.

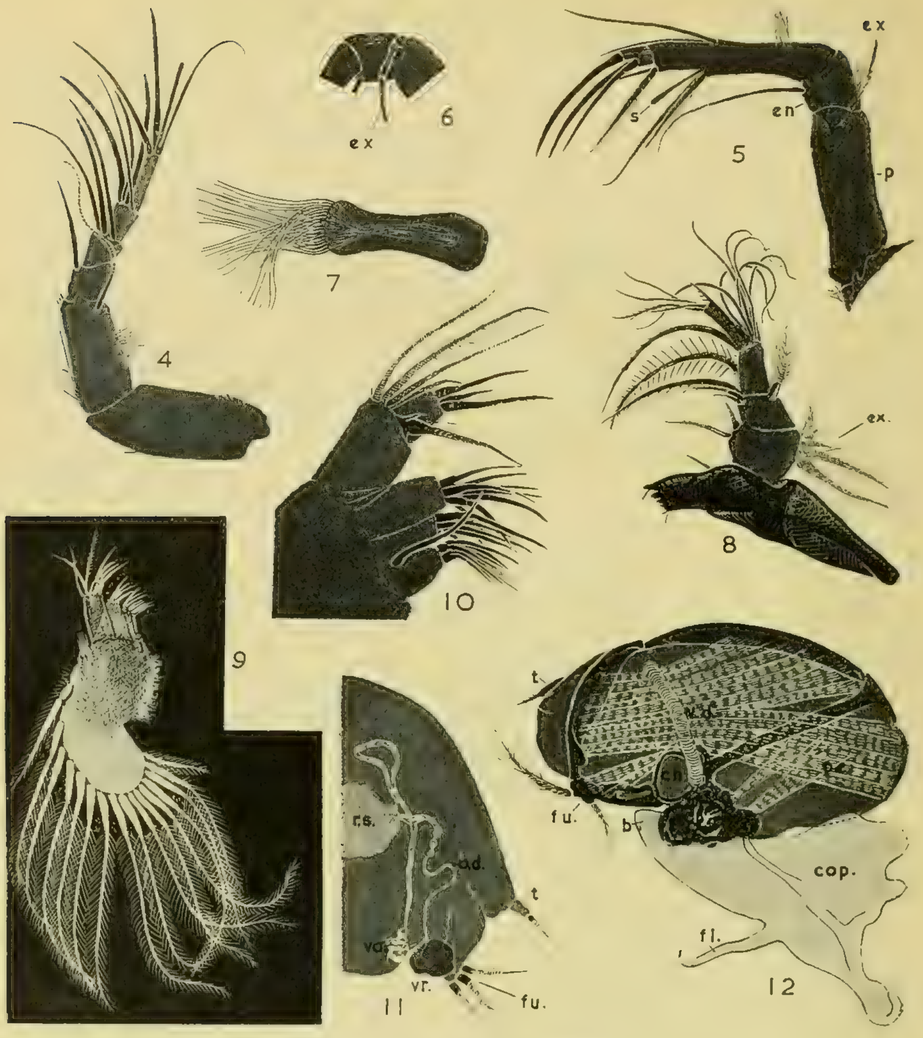
In both valves a hollow lying immediately below and in front of the anterior hinge element leads to the eye tubercle, and is for the reception of the eye of the animal. The tubercle, being highly polished and transparent, perhaps serves as a primitive lens.

The first antenna (Text-fig. 4) consists of six segments and is the same in both sexes. The proportionate lengths of the segments and of the various setae, spines and sense organs are best indicated by the drawing. The first segment has a tuft of long spinules on the posterior face near the base. The second segment has a few spinules on both posterior and anterior faces, and on the postero-distal corner there is a slender, flexible, finely-haired seta. The third segment has a tapering seta on the antero-distal corner. The fourth segment has two smooth setae on the antero-distal corner, one stout and the other more slender, and from the middle of the distal edge on the medial side is a smooth, slender seta. The fifth segment has two stout setae and a slender one near the antero-distal corner, and one slender one on the distal edge on the medial side. These four are all smooth. The last segment has two stout terminal setae; and a slender one which is united at its base to a sense club (*s.*).

The second antenna (Text-figs. 5 and 6) consists of a protopod (*p.*) of one segment, an endopod (*en.*) of three segments, and a very small exopod (*ex.*) of two segments, and is alike in both sexes except for the small differences in the exopod. The protopod is quite unarmed. The exopod is reduced to what appears to be a sense organ. This is best developed in the female (Fig. 6), where it is very thinly chitinized and rather broad, and is less than twice the length of the first segment of the endopod. In the male (Text-fig. 5) the exopod is shorter still and looks very like an ordinary seta. Brady (1898) describes the exopod as " a very short, falcate, urticating seta [in the female], which is absent in the male."

The first segment of the endopod bears some stiff bristles and a long slender seta with very minute hairs on the postero-distal corner. The second segment of the endopod bears a tuft of hair-like spinules on its first quarter on the inner side. About two-thirds along its length there are two smooth setae on its anterior face, and on the posterior face at about this level there is one stout, tapering seta, and one longer but more slender one, both feathered, and near them a sense club (*s.*). At the postero-distal corner of this segment there is one stout, feathered seta and one small naked one. The last segment has three stout, naked setae, two together half-way along its posterior margin and the other one terminal.

The mandible (Text-fig. 8) is the same in both sexes. The shape of the basal biting part is shown in the figure. The biting edge contains six strong teeth each with a secondary cusp. The most anterior of these teeth is the largest, and they decrease in size gradually towards the posterior corner ; the first two take up half the biting edge. There is a bristle between the first and second and another between the second and third teeth, and on the posterior medial corner beyond the largest tooth there are two ribbon-like bifurcate setae which are about twice the length of



TEXT-FIGS. 4–12. *Trachyleberis lytteltonensis* sp. nov.

Fig. 4, first antenna, × 130. Fig. 5, second antenna of male, × 130. Fig. 6, part of second antenna of female with exopod, × 180. Fig. 7, brush-shaped organ of male, right member from behind, × 360. Fig. 8, right mandible from inner side, × 130. Fig. 9, left maxilla from outer side, × 130. Fig. 10, palp and endites of left maxilla from outer side, × 220. Fig. 11, posterior part of body of female, × 180. Fig. 12, posterior part of body and copulatory apparatus of male, × 130. *b.*, postero-ventral corner of copulatory appendage; *ch.*, chamber; *cop.*, copulatory appendage; *en.*, endopod; *ex.*, exopod; *fl.*, flagellum; *fu.*, furcal ramus; *ly.*, labyrinth; *od.*, oviduct; *p.*, protopod; *pe.*, penis; *r.s.*, receptaculum seminis; *s.*, sense club; *t.*, terminal seta; *va.*, vagina; *v.d.*, vas deferens; *vr.*, verruca.

the teeth near them. Beyond them again there is a single bent seta. Between the biting edge and the palp there is a seta with a few hairs.

The palp consists of the second segment of the protopod bearing a three-segmented endopod and an exopod of one segment. The exopod rises from the dorsal part of the outer face of the protopod and is directed distally. It consists of a single rounded segment narrow at its base, with five carrot-shaped, hairy setae which are thinly chitinized and of very different lengths, as shown in the figure.

The ventral margin of the protopod carries two delicate setae. The one nearest the distal corner is more or less parallel to the endopod and is shorter and stouter than the other. Both are annulated and hairy.

The first segment of the endopod has an annulated hairy seta on the inside of the distal dorsal corner, and on the ventral distal corner there are four setae, of which the two medial ones are small. The two on the outer side are stout and curved and are armed with long, stiff hairs which are rather wide apart. In preparations these are most evident in the outer seta, in which the hairs lie parallel to the cover slip. On the dorsal part of the distal end of the next segment is a group of seven whip-like, flexible, naked setae, and on the ventral distal corner there is a long tapering seta with hairs. On the medial side in the middle of the distal edge there is a seta which is a little longer than the terminal segment and has a few stiff hairs on the ventral side.

The terminal segment of the endopod is a little longer than the preceding one, but rather less than half its diameter and slightly tapering. It has four slender terminal setae, one of which has hairs.

The maxilla (Text-figs. 9, 10) is the same in both sexes. Between the long, plumose setae of the vibratory plate and the palp on the distal edge of the appendage there is a hairy swelling with a group of bristles directed parallel to the palp. The first of the 16 plumose setae arises from this swelling. This seta is constricted into two parts, both of which are rather swollen. The distal part tapers to a point. The second to the fifteenth plumose setae are longer and very much alike. They have a swollen basal part rather longer than the corresponding basal part of the first seta, and the distal part is not swollen but long and feathered. The sixteenth seta is much smaller than the others but hardly longer than the basal part of the middle 14, and it appears to be of one piece without a constriction.

The palp is composed of two more or less cylindrical segments, the first segment being about twice the length and twice the width of the second. On the distal edge of the first segment and dorsal to the second segment are four slender setae differing from each other in hairiness. That next to the second segment is the shortest, being about twice the length of the second segment ; it has minute hairs all round it. The other three setae are all nearly twice this length ; one appears to be naked, the second has rather short hairs, and the other has long hairs ; these three are annulated for the distal part of their length. In addition to these setae, the distal margin of the first segment carries a seta near the outer face of the second segment. This seta has a swollen base from which arises a short secondary setule.

There are three distinct endites, the first, i.e., the one nearest the palp, bears terminally eight tapering setae, many of which have swollen bases. These are all naked or nearly so. The two other endites have several pointed terminal setae, the actual number being difficult to determine. In addition to these terminal setae, the last endite has a fairly long seta arising from near its base on the side facing the palp.

The fifth, sixth and seventh pairs of appendages are basically similar to one another. They are all leg-like, and will be referred to here as the first, second and third pairs of legs. Each of the three pairs shows sexual dimorphism, and furthermore, in the first pair of legs of the male the right leg differs from the left leg. The following description will apply to both sides and both sexes unless otherwise indicated.

The first leg (Text-figs. 13–15) consists of four segments. The first segment has two annulated setae on the anterior margin and two on the antero-distal corner overhanging the knee-like joint. Near the base of the leg on the posterior side there is a soft, hairy, carrot-shaped seta, and near it along the posterior margin of the segment there are some long hairs. The postero-distal corner of the first segment has a hollow surrounded by fine spinules. The second segment broadens distally and carries one seta. This is on the antero-distal corner in the female (Text-fig. 13), and carries short hairs. In the male this seta is more hairy and placed on the anterior margin short of the corner, and is farther from the corner on the right leg (Text-fig. 14) than on the left (Text-fig. 15). Apart from a few minute spinules the right leg of the male bears nothing else on the second segment, but on the left leg of the male there is a swelling in about the middle of the anterior margin. This carries a roughened friction pad on the medial side and a hairy boss on the outer side. In the female (Text-fig. 13) there is a group of spinules on this part of the anterior margin. The third and fourth segments of the leg are the same in both sexes and on both sides. The distal edge of each segment is armed with small spinules on both sides ; these are much longer laterally than medially. The terminal curved claw is about twice the length of the last segment and is smooth in the male and pectinate on the inside of the curve in the female.

The second pair of legs (Text-figs. 16, 17) is sexually dimorphic, but in the male as well as in the female the left and right legs form a symmetrical pair. The first segment is the same in both sexes, and has similar setae to those of the first leg except that only one seta overhangs the " knee." The second segment broadens gradually distally, and is nearly as long as the first segment but much narrower. It bears an annulated seta on the antero-distal corner, and in the male (Text-fig. 17) three groups of stiff, sharply-pointed bristles ; in the female (Text-fig. 16) only the most proximal of these three groups is present. The third and fourth segments are similar to those of the first leg but rather longer and more slenderly built. The claw is smooth in the male and pectinate in the female.

The third pair of legs (Text-figs. 18, 19) is essentially similar to the second pair. The first segment has a normal annulated seta on the postero-proximal corner instead of the carrot-shaped seta. In the male the second segment has four groups of conspicuous, straight, sharply-pointed bristles on the anterior margin ; only the two most proximal of these groups are represented in the female, and in this sex the bristles are more flexible. The seta on the antero-distal corner is long, and in the male, crooked. The male has a group of slender-pointed spines on the middle of the anterior margin of the last segment. The terminal claw is pectinate in both sexes.

The copulatory apparatus is of the usual complex nature. Specimens were unfortunately not well enough preserved for the details of the softer parts to be made out. The structure of the less easily macerated parts is shown in Text-fig. 12. The following features were found in each of five males examined. On each side the apparatus consists of two parts, a roughly oval muscular part called by Skogsberg (1928) and others the " penis " (*pe.*) and a distal triangular " copulatory appendage " (*cop.*). The muscular part contains a number of chitinous struts with muscles running between them as shown. Near the base of the copulatory appendage there is a very complex labyrinth (*ly.*) with a rounded chamber (*ch.*) which has chitinous walls. A tube with spirally thickened walls, presumably the vas deferens (*v.d.*), runs to this chamber. The other end of the tube was found in very different positions in different specimens, having apparently become free as a result of maceration of the soft parts ; but the position figured is believed to be correct. The copulatory appendage is a thin-walled, roughly triangular organ with irregular outgrowths from its broader distal part. These outgrowths are roughly similar on both sides ; but those of the same side of two different individuals are usually more alike than the right and left ones of the same individual. The appendage on the right has a flagellum (*fl.*) which is absent on the left. The "postero-ventral" part of the copulatory appendage ends with a rounded point (*b.*). We were unable to determine a ductus ejaculatorius.

The female reproductive system and the shape of the posterior part of the body are shown in Text-fig. 11. On each side of the body near the caudal furca, which in this sex has three setae, lies the verruca (*vr.*). The oviduct (*od.*) is a sinuous tube connected with the verruca. The vagina (*va.*) is separate from the oviduct and opens anterior to it. Both these ducts are connected with the receptaculum seminis (*r.s.*). The receptaculum and the other organs are all paired.

The paired brush-shaped organs of the male (Text-fig. 7) are placed on the ventral side of the body between the " knees " of the first pair of legs.

The furcal rami (*fu.*) are reduced to a simple swelling on each side bearing three setae in the female and two setae in the male. In both sexes the hindermost part of the body bears a single median seta (*t.*).

Trachyleberis scabrocuneata (Brady)

(Text-figs. 20–25 ; Pl. 1, figs. 5, 6, 8 ; Pl. 2, figs. 5, 6, 9, 10.)

Cythere scabrocuneata Brady, 1880, Challenger Rep. **1** : 103, pl. 17, figs. 5a–f ; pl. 23, figs. 2a–c.

Not *Trachyleberis scabrocuneata*, Brady, 1898, Trans. zool. Soc. Lond. **14** : 444, pl. 47, figs. 1–7, 18–25.

Trachyleberis scabrocuneata, Sylvester-Bradley, 1948, J. Paleont. **22** : 794, pl. 122, figs. 13–18.

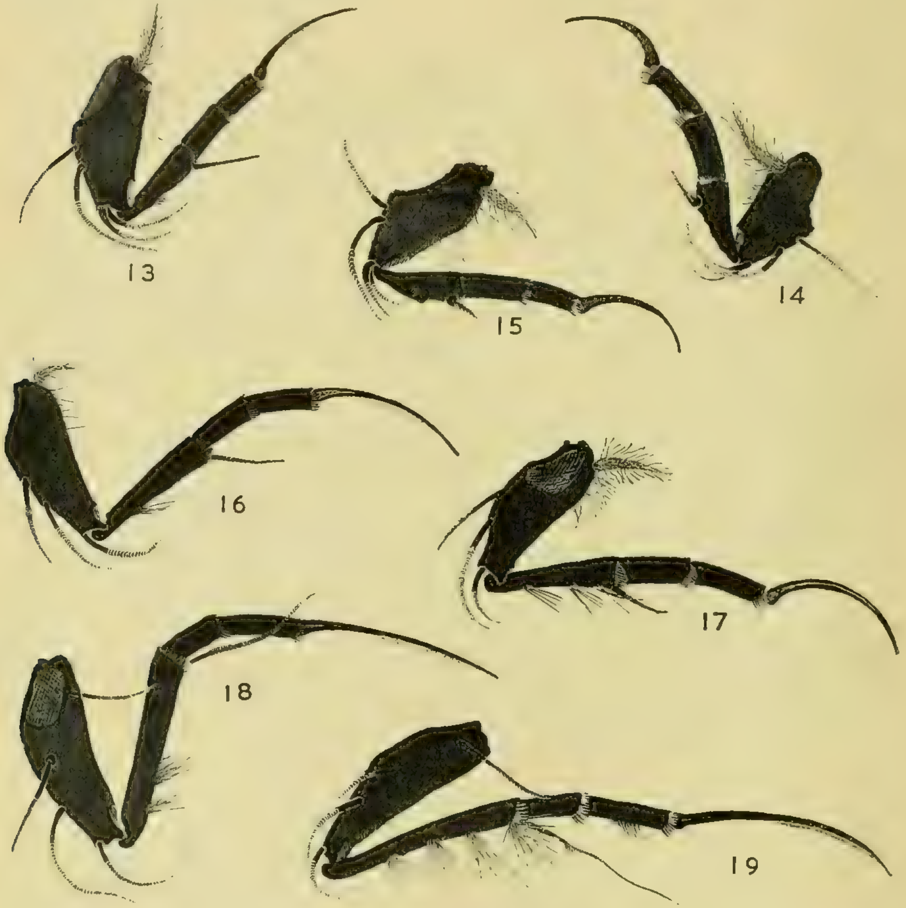
Not *Trachyleberis scabrocuneata*, Hornibrook, 1952, New Zealand Geol. Surv., Palaeont. Bull. **18** : 32–33, pl. 3, figs. 38, 39, 48.

Occurrence and Material. The only material that has survived is that dredged by the "Challenger" Expedition from the Inland Sea of Japan at 14 fathoms. The following specimens are held in the British Museum (Nat. Hist.):

Lectotype (here chosen) B.M. 1952.12.10.1, 2.

Paratypes: B.M. 1948.3.10.1–5, B.M. 1952.12.10.3–9.

Other Records. Brady's other records of this species are suspected to be *T. lytteltonensis* or other species.



Text-figs. 13–19. *Trachyleberis lytteltonensis* sp. nov.

Fig. 13, left first leg of female, × 180. Fig. 14, right first leg of male, × 145. Fig. 15, left first leg of male, × 145. Fig. 16, left second leg of female, × 180. Fig. 17, left second leg of male, × 145. Fig. 18, left third leg of female, × 180. Fig. 19, left third leg of male, × 145.

Description. The shell of this species has been previously described (Sylvester-Bradley, 1948*b*) on the basis of the type material here re-examined, and only such details as serve to distinguish the species from *T. lytteltonensis* need be dealt with again. The shell of the species has been refigured on Pls. 1 and 2 to aid comparison.

There are no differences to report in the general shape of the carapace, the degree of sexual dimorphy, or the size. In the following table of dimensions and proportions, those of the complete carapaces have been estimated from single valves :

		Length	Height	Width
Dimensions :	♂ B.M. 1948.3.10.1 .	1·10 mm.	0·52 mm.	0·49 mm.
	♀ B.M. 1948.3.10.5 .	0·90 ,,	0·46 ,,	0·46 ,,
Proportions :	♂ B.M. 1948.3.10.1 .	2·13	1	0·94
	♀ B.M. 1948.3.10.5 .	1·94	1	1·00

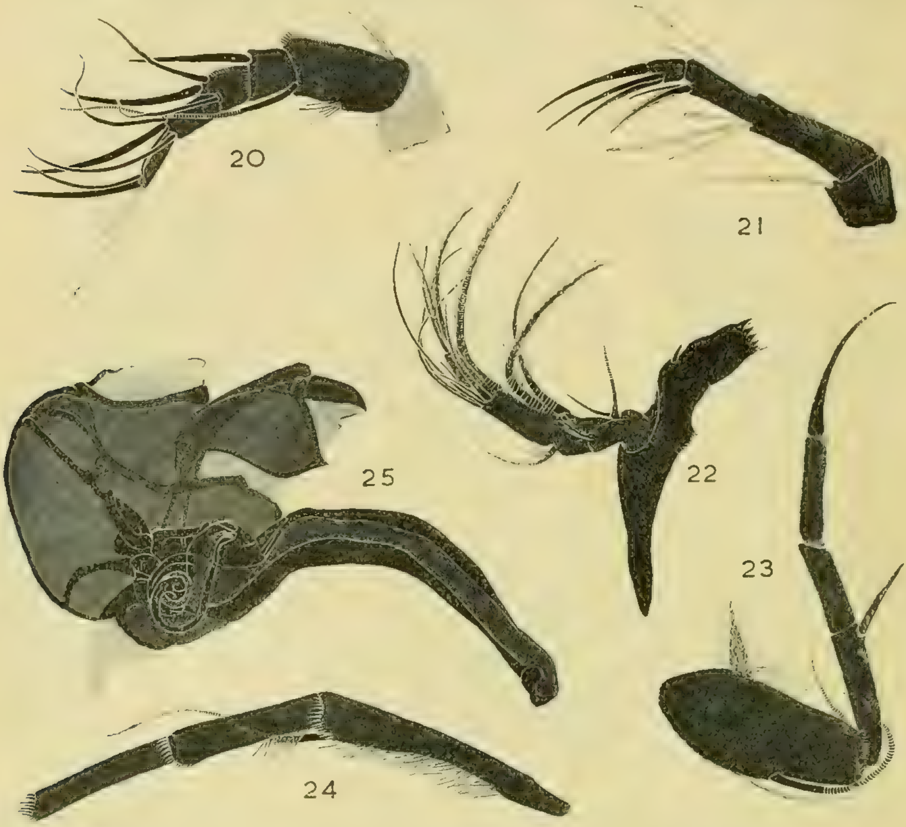
The antero-dorsal complex of *T. scabrocuneata* (Pl. 1, figs. 5, 6, 8) consists of a sharp ridge running from the eye tubercle forwards and downwards to as far as the median line, and presents an immediate contrast to the rounded swelling which forms the antero-dorsal complex of *T. lytteltonensis*. Similarly the sub-central tubercle of *T. scabrocuneata* is surmounted by ridge-like elevations rather than the mammillae of *T. lytteltonensis*. The general style of ornament is similar in the two species, but the tubercles in *T. scabrocuneata* are smaller, more sharply defined and greater in number than in *T. lytteltonensis*. In *T. scabrocuneata* the marginal spines in the postero-ventral region, forming a ventral ridge, are compressed and blade-like, and swell out above the base (Pl. 2, figs. 9 and 10). It is interesting to note that a third species, *T. thomsoni* Hornibrook, 1952, ranging in New Zealand from the Paleocene (Waipawan) to Recent, as shown by Hornibrook's figures, is also similar in style of ornament, but the tubercles are even fewer, and are more pronounced, rising from dorsal and ventral ridges as veritable spines.

The internal characters of the carapace (Pl. 2, figs. 5, 6, 9 and 10) are essentially similar to those displayed by *T. lytteltonensis*. The anterior tooth of the right valve, however, projects far more strongly above its base than that of *T. lytteltonensis* (Pl. 2, fig. 6).

The first antenna of the female is shown in Text-fig. 20. This drawing has been made with the aid of a camera lucida, but antennules from three separate females have been used in order to include as many setae as possible. In none of the specimens was the basal segment or the terminal seta with attached sense club present. Lightly stippled " ghosts " of these have been added to the drawings by analogy with the other species. As will be seen by comparing Text-fig. 20 with Text-fig. 4 the first antennae of the two species are practically identical. The second antennae also appear to be identical in the two species (compare Text-fig. 21 with Text-fig. 5). Only the three terminal segments of this appendage with the five most terminal setae are preserved, however, and we could find no exopod.

The mandible (Text-fig. 22) is similar in the two species, though the palp has less than seven whip-like setae on the posterior side of the penultimate segment, but this may have been because some of the setae had been lost. The palps of two mandibles were recovered, but unfortunately in both examples the first segment of the palp was rather distorted and in neither was it possible to see the exopod.

A number of parts of the legs were preserved, but the only complete one is the second left leg of a female shown in Text-fig. 23. Instead of the group of bristles present on the proximal third of the second segment as in *T. lytteltonensis*, there are two groups of short spinules placed laterally. Otherwise there seems to be no difference of any importance. Three segments of the third right leg of the male



TEXT-FIGS. 20–25. *Trachyleberis scabrocuneata* Brady. Type material.

Fig. 20, first antenna of female, × 165, drawn from three specimens. Fig. 21, second antenna, × 165, from two specimens. Fig. 22, mandible, × 165. Fig. 23, second leg of female, × 260. Fig. 24, three segments of the third leg of a male, × 260. Fig. 25, copulatory apparatus of male, × 260, drawn from three specimens.

Segments and setae shown lightly stippled were missing in the specimens seen, and have been added by analogy with the other species.

are shown in Text-fig. 24. These are very similar to the corresponding segments of *T. lytteltonensis* (Text-fig. 22), and the ventral margins of the second and third segments are hairy. These hairs, however, do not seem to be arranged in distinct groups as they are in *T. lytteltonensis*.

The copulatory apparatus (Text-fig. 25), of which no less than three specimens were preserved, is quite unlike that of *T. lytteltonensis* (compare Text-fig. 25 with Text-fig. 12). None of the three specimens was sufficiently well-preserved to show the muscles, but all three were remarkably like one another ; two of the three were right- and left-hand members of one specimen. The apparatus in the two species is so different that it is difficult to homologize the parts. In *T. scabrocuneata* there is a distinctly spiral ejaculatory duct which could not be seen in *T. lytteltonensis*. The distal parts of the copulatory appendage in *T. scabrocuneata* is a long, rather curved organ with heavily chitinized walls, as shown in the figure, and very different from the broadly expanded, laminate and delicately-built organ of *T. lytteltonensis*.

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EXPLANATION OF PLATES

PLATE 1

All external lateral views. All figures except fig. 7 from retouched photographs of specimens coated with magnesium oxide, × 60. Fig. 7 from an unretouched photograph, × 120, of a specimen immersed in benzyl alcohol and illuminated by transmitted light.

FIGS. 1–4, 7. *Trachyleberis lytteltonensis* sp. nov. Figs. 1, 2, B.M. 1952.12.9.1 (♂) ; figs. 3, 4, 7, B.M. 1952.12.9.6 (♀).

FIGS. 5, 6, 8. *Trachyleberis scabrocuneata* (Brady). Fig. 5, B.M. 1948.3.10.1 (♂) ; fig. 6, B.M. 1948.3.10.2 (♂) ; fig. 8, B.M. 1948.3.10.5 (♀).

PLATE 2

All figures are from retouched photographs, × 60. Figs. 1–6, dorsal views ; figs. 7–10, internal lateral views.

FIGS. 1–4, 7, 8. *Trachyleberis lytteltonensis* sp. nov. Figs. 1, 2 B.M. 1952.12.9.1 (♂) ; figs. 3, 4, 7, 8, B.M. 1952.12.9.6 (♀).

FIGS. 5, 6, 9, 10. *Trachyleberis scabrocuneata* (Brady). Figs. 5, 9, B.M. 1948.3.10.1 (♂) ; figs. 6, 10, B.M. 1948.3.10.5 (♀).

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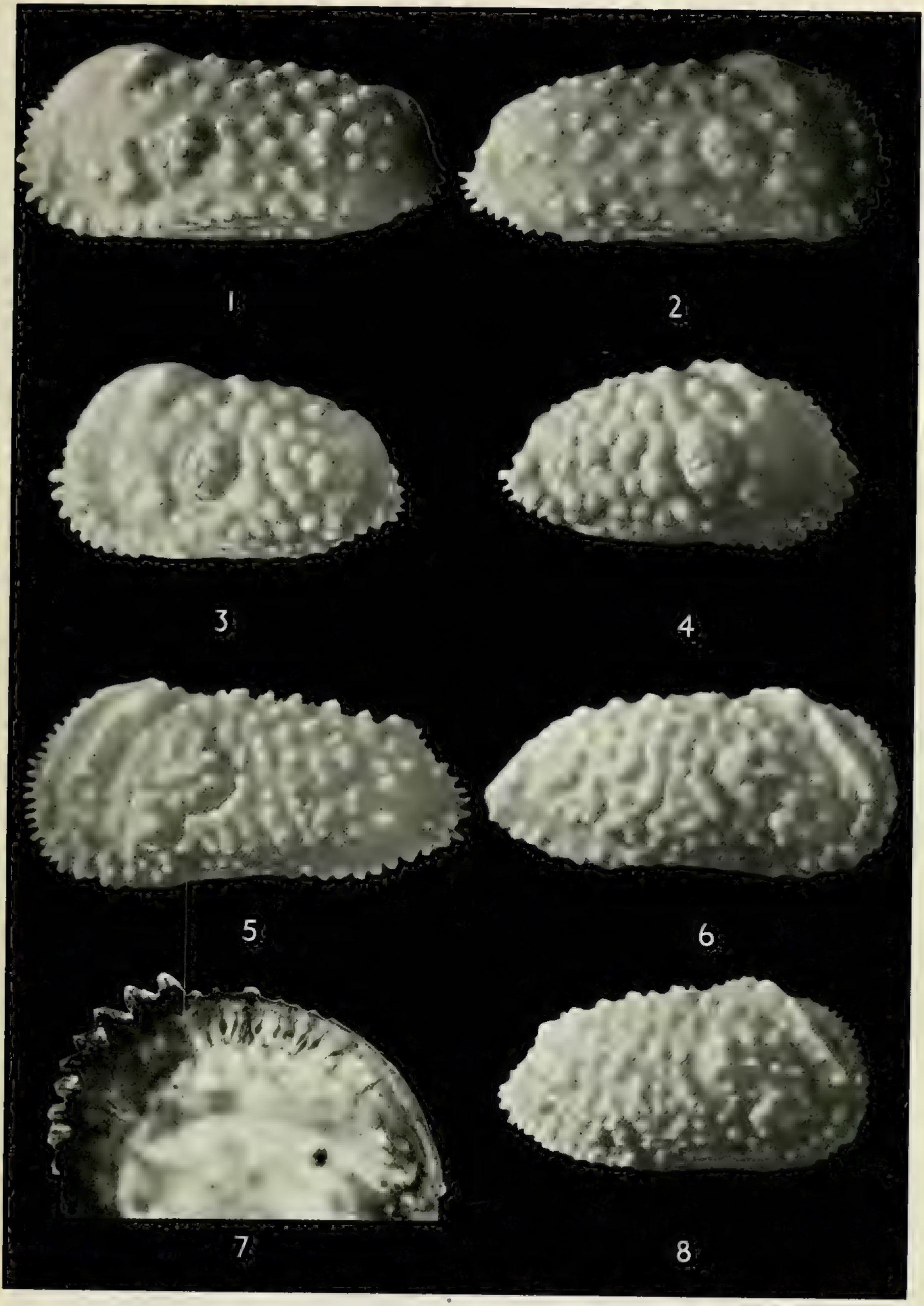

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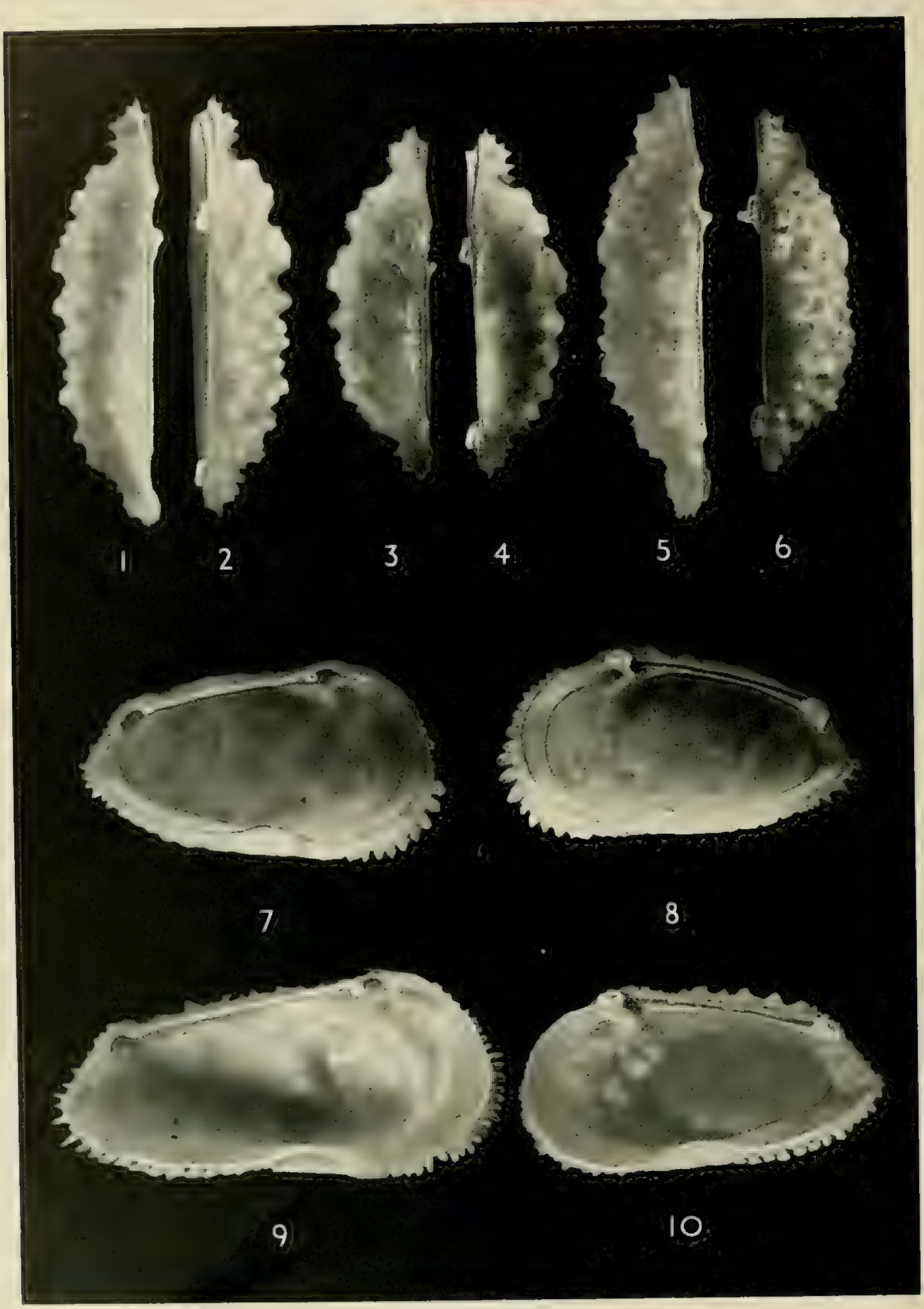
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ISABELLA GORDON

BULLETIN OF
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ZOOLOGY Vol. 2 No. 2
LONDON: 1953

ON THE PUERULUS STAGE OF SOME SPINY LOBSTERS (PALINURIDAE)

PRESENTED
13 MAR 1953

BY
ISABELLA GORDON, D.Sc., Ph.D.
British Museum (Nat. Hist.)

Pp. 17–42 ; *9 Text-figures*

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ON THE PUERULUS STAGE OF SOME SPINY LOBSTERS (PALINURIDAE)

By ISABELLA GORDON

SYNOPSIS

The paper includes a key to the determination of the adult Palinurid genera to which the known post-larvae are referable, descriptions and figures of the Puerulus stage of several species of the genus *Panulirus* and notes on the Puerulus of the European Spiny Lobster. In an appendix the range of variation in the adults of the species *Panulirus homarus* (L.) is discussed.

INTRODUCTION

In March, 1952, I received from Hugh Copley, Esq., Fish Warden, Nairobi, an almost complete and beautifully preserved specimen of the Puerulus stage of a Palinurid. The antennae were intact, and the most striking feature of the post-larva was the dark brown spatulate apex of the long flagellum. A very similar Puerulus has recently been described in a Japanese journal which is not yet available in this country ; as the text is mostly in Japanese a description in English seems essential. A number of Pueruli from the Marquesas and Coiba were found in undetermined collections in the British Museum and they are also described in the following short paper. All these post-larvae proved to belong to the genus *Panulirus*, and it has been possible to refer most of them to their respective adult species. All possess a pair of long, backwardly directed spines at the posterolateral angles of the thoracic sternum (near the bases of the last pair of walking legs). All agree, moreover, in having the exopodite of maxilliped 3 vestigial, and therefore belong to species in which that exopodite is lacking in the adult. The material from the Marquesas is referable to either *Panulirus homarus* (L.) or the closely related *P. dasypus* (Latr.) and, in an appendix, I discuss my reasons for believing that these two may belong to one variable species.

In the Puerulus referred to *P. argus* (Latr.) by Gurney (1942, p. 234, fig. 93) the posterolateral thoracic spines are replaced by blunt nodules, and the exopodite of maxilliped 3 is rather longer than the ischium of the endopodite. The posterolateral spines are absent in *Puerulus pellucidus* (Ortmann), which has been referred to *Panulirus japonicus* (von Siebold)—see synonymy in Holthuis, 1946, p. 111, and Nakazawa, 1917.

At the present time the post-larva is known for only four genera of the Palinuridae, namely, *Palinurus* Fabr., *Panulirus* White, *Jasus* Parker and *Justitia* Holthuis. I have examined Pueruli belonging to each of the first three genera but that of *Justitia* is known only from a single specimen collected by the " Blake." It was first described as the " *Puerulus* d'Agassiz," referable to *Palinurus longimanus* H. M.-Edw. by Bouvier (1913, pp. 82 and 87 ; 1914, p. 187 ; and 1925,

p. 442, pl. 8, fig. 1), and Bouvier's figure has been reproduced by Schmitt (1935, p. 173, fig. 37). Holthuis erected the genus *Justitia* for *J. longimana* (H. M.-Edw.) and its variety *mauritiana* (Miers) in 1946, p. 115.

In the British Museum collection are the three specimens—Phyllosoma, Phyllosoma with the Puerulus in the act of disengaging itself, and Puerulus—of *Palinurus vulgaris* Latr. figured by Bouvier (1914, figs. 1, 2, and 3–6). Bouvier's sketch of the carapace of the Puerulus is not very accurate as to the anterior spines, the supraorbital spines especially being much more prominent than in the actual specimen (reg. no. 1914.12.17.4). I take this opportunity of refiguring the anterior part of the carapace and the antennule (Fig. 1*a*, *b* and *c*) for comparison with those of *Jasus* (Fig. 1*d* and *e*) and of *Justitia* as figured in Bouvier, 1925, pl. 8, fig. 1 (which appears to be accurate). Incidentally, Holthuis says that the common European "langouste" should be known as *Palinurus elephas* (Fabr.), which antedates *vulgaris* Latr.

I also give a key to the determination of the adult genera to which the post-larvae are referable ; it is more detailed than that given by Bouvier (1913, p. 87), but for the characters of the Puerulus of *Justitia* I have had to rely on Bouvier's figure and descriptions. I am not sure whether the antennae are intact, but if so they do not exceed 1·5 times the body length.

KEY TO THE DETERMINATION OF THE ADULT GENERA TO WHICH THE POST-LARVAE ARE REFERABLE

I. Antennular flagella distinctly shorter than the peduncle, outer much more robust than the inner (Fig. 1*a* and *d*). Anterior margin of the antennular[1] tergum much narrower than the space between the tips of the supraorbital spines. Rostrum well formed or rudimentary (Fig. 1*a* and *d*). The "brevicornis" group.

A. Exopodite of maxilliped 3 long, with multi-segmented flagellum. Posterolateral spines present on several of the somites of thoracic sternum. Rostrum rudimentary.

1. Supraorbital spines denticulate on upper margin ; plate formed by these spines and the rostrum broad and advanced so as to conceal the eye-stalks, the corneae visible laterally. Three pairs of spinules on thoracic sternum. Distinct median carina on carapace and abdominal somites 2–5. Only a few spines on carapace near the orbits. Second segment of antennular peduncle equal to third *Justitia* Holthuis.

---

[1] The antennal tergum of some authors.

FIG. 1. *Palinurus elephas* (Fabr.) – *vulgaris* Latr. The Puerulus figured by Bouvier, 1914, p. 288, fig. 6. (*c.l.* = 7·5 mm.). *a.* Anterior part of carapace, in dorsal aspect, with left antennule and antennal peduncle. *b.* Right anterolateral spine with the two spines immediately behind it, more magnified. *c.* Left antennule more magnified. *Jasus lalandei* (H. M.-Edw.). Puerulus from "Discovery" Stn. 101, 15/x/26 (*c.l.* = 9·5 mm.). *d.* Anterior part of carapace in dorsal aspect, with left antennule and antennal peduncle. *e.* Left antennule more magnified.

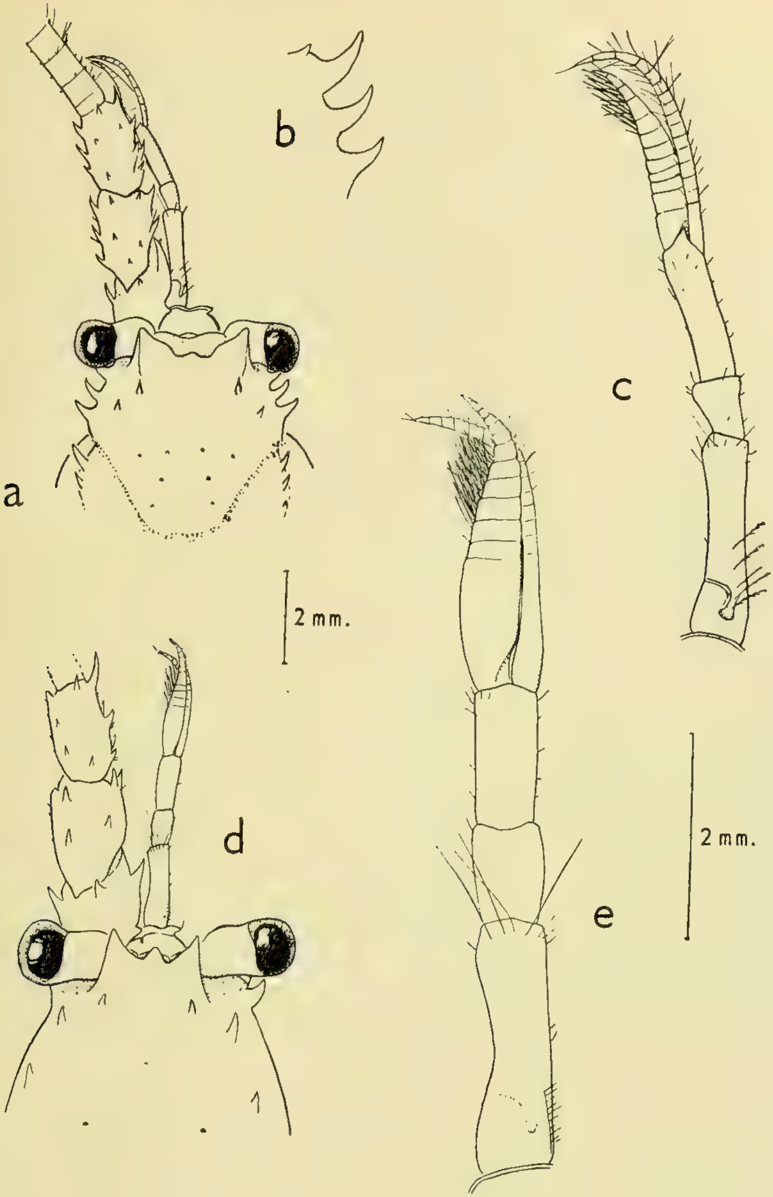

b
a
2 mm.
c
d
e
2 mm.

Fig. 1.

2. Supraorbital spines not denticulate on upper margin ; plate formed by these spines and the rostrum narrower and less advanced, most of eye-stalks visible (Fig. 1*a*). Four pairs of spinules on thoracic sternum. No median carina on carapace or abdomen. Carapace spiny, three spines at each anterolateral angle and a longitudinal row of spinules replacing each lateral carina. Second segment of antennular peduncle shorter than third (Fig. 1*c*). [Antenna not quite 1·5 times the body length and tapering distally. First pair of pereiopods more robust than the others.] . . *Palinurus* Fabr.

B. Exopodite of maxilliped 3 short, without flagellum. No posterolateral spines on thoracic sternum. Rostrum well developed (Fig. 1*d*). [Supraorbital spines not denticulate on upper margin ; plate formed by these and the rostrum narrow, moderately advanced, but most of eye-stalks visible. One spine at anterolateral angle of carapace. No median, but two lateral carinae on posterior two-thirds of carapace. Second segment of antennular peduncle rather shorter than third (Fig. 1*e*). Antenna not quite 1·5 times the body length and tapering distally. First pair of pereiopods more robust than the others.] . . . . *Jasus* Parker.

II. Antennular flagella at least as long as the peduncle, outer not much more robust than the inner (Figs. 2*a*, 5*a*, *c*). Anterior margin of antennular[1] tergum as wide as the space between the tips of the supraorbital spines. Rostrum absent. The " longicornis " group. [Usually a large pair of posterolateral spines on last somite of thoracic sternum and three carinae on the carapace. One (occasionally two) spine(s) at anterolateral angle of carapace. Second segment of antennular peduncle equal to third. First pair of pereiopods not more robust than the others (Fig. 7*b*, *c*).] . *Panulirus* White.

a. THE PUERULUS STAGE OR POST-LARVA OF PANULIRUS SP.

(Figs. 2*a* ; 3 ; 7*c*)

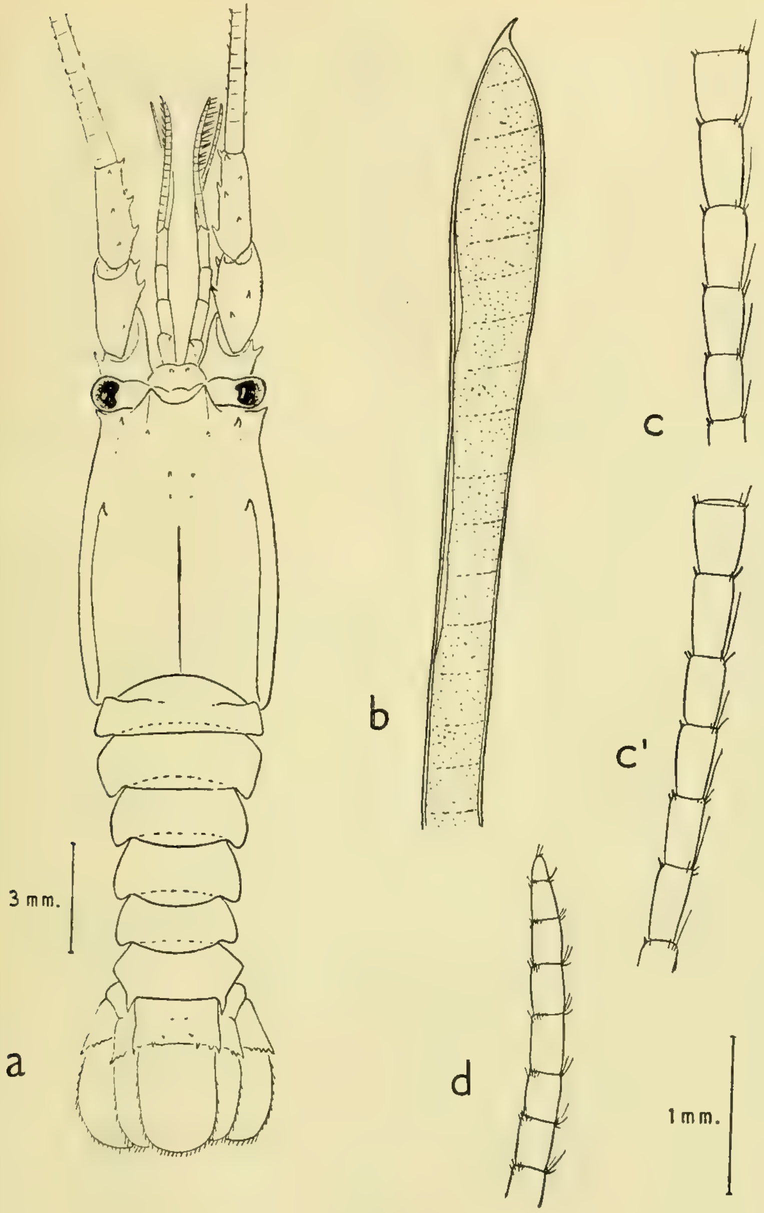
MATERIAL. Taken in trawl by M.F.V. " Menika " on Leopold Reef ground, Malindi, Kenya Colony, in 10 to 20 fms.—one specimen, presented by H. Copley, Esq., Fish Warden, Nairobi. March, 1952.

Measurements : Length of body 21·5 mm. ; Length of carapace 8 mm. ; Length of antenna (complete) 45 mm.

DESCRIPTION. The specimen had been preserved in formalin and the body, though transparent in life, was apparently tinged with reddish brown. When received it was complete except that pereiopods II and V on the right side were missing. The most striking feature of the post-larva is the enormously long antennae, measuring just over twice the body length. The flagellum ends in a flattened oar-like expansion which is all the more conspicuous because the last 7 or 8 segments of the spatula are brown in colour (Fig. 3*a* ; brown portion stippled). A narrow

[1] See footnote on p. 18.

FIG. 2. *a*. Puerulus of *Panulirus* sp. from Kenya, in dorsal aspect, most of the antennal flagella omitted. *b*. Distal portion of antenna of the last stage Phyllosoma of *P. homarus* (L.) from the Marquesas. *c* and *c′*. Distal segments of incomplete antennal flagella of two Pueruli of *P. homarus* (L.) from the Marquesas. *d*. Terminal segments of antennal flagellum of the Puerulus of *P. argus* (Latr.) from Bermuda.


a
b
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c'
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3 mm.
1 mm.

FIG. 2.

band of the brown colour, a trifle paler, is present about one-third of the way along the flagellum (i.e., at distal end of proximal third).

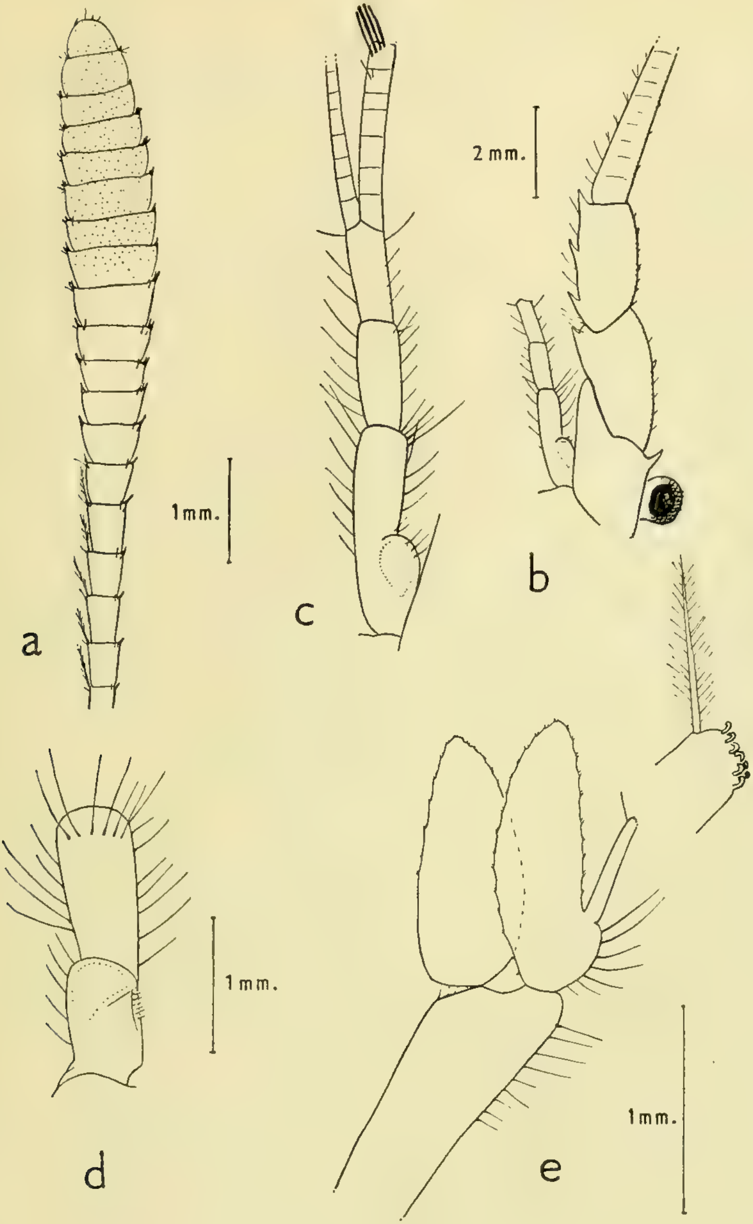
Fig. 2*a* represents the post-larva in dorsal aspect, with the greater part of the antennal flagella omitted. The *carapace* measures 8 mm. from the tip of the supraorbital spine to the posterior margin ; it bears only two pairs of spinules in addition to that at each anterolateral angle. The anterior pair is situated immediately behind the eyes ; the posterior pair is some distance behind, one spinule at the anterior end of each lateral carina. If the specimen is examined carefully under a binocular microscope, three pairs of incipient spinules can be detected situated between the anterior and posterior pairs of spinules, i.e., two median (gastric) pairs a short distance in front of the median carina, and another pair posterior to the carinae on the supraorbital spines. The three longitudinal carinae on the posterior two-thirds of the carapace are not very clearly seen in dorsal aspect, but in profile they stand out clearly : Each lateral carina seems to be continued forwards to the anterior pair of spinules ; the incipient spinules appear as thickenings of the chitin, so that the median carina seems to bifurcate and to be continued forwards to the base of each rostral horn. A pair of incipient spinules is present on the antennular tergum, near the anterior margin. A thin carina, not visible in dorsal aspect, runs parallel to the lateral edge of the carapace. The cervical furrow is not very apparent at this stage.

The *thoracic sternum* is very similar to that of the Puerulus of *Panulirus regius* B. Capello figured by Bouvier (1917, pl. ix, fig. 9) ; in addition to the pair of large, backwardly-directed spines on the last somite, near the bases of pereiopods V, there are blunt lobules, which diminish in size anteriorly, at the postero-lateral angles of each of the three preceding somites. Bouvier's fig. 9 does not show these, but that on the penultimate somite is visible in lateral aspect in his fig. 10. The thoracic ganglia are clearly visible through the thin integument.

The *abdomen* and tail fan present no unusual features. No groove is present on any of the terga parallel to the posterior margin, but the anterior margin of the succeeding somite is visible through the thin chitin and is represented by a broken line in Fig. 2*a*. The pleura of somites 2 to 6 each possesses a sharp, backwardly directed spine which is not visible in dorsal aspect.

The *antennule* is short, extending only a little way beyond the antennal peduncle (Fig. 2*a*) ; the external flagellum is the more robust, a trifle longer than the internal and beset with special sensory setae on all but the proximal 6 or 7 segments. Each flagellum has 18 or 19 segments. The details of the peduncle are shown in ventrolateral aspect in Fig. 3*b* and *c*, of the basal segment in dorsal aspect in Fig. 3*d*. All the setae are very finely plumose, as are those forming what Gilchrist (1920, p. 198, fig. 13) calls the " antennular screen." In the Puerulus of *Jasus lalandei* (H. M. Edw.) Gilchrist shows these setae as heavily plumose. The basal segment

FIG. 3. Puerulus of *Panulirus* sp. from Kenya. *a*. Terminal portion of antennal flagellum, to show the spatulate apex. *b*. Antennal and antennular peduncles, in ventrolateral aspect. *c*. The latter further enlarged. *d*. Basal segment of antennular peduncle, in dorsal aspect. *e*. Pleopod on second abdominal somite, with most of the long setae omitted, and apex of *appendix interna* further enlarged.


a
1mm.
c
2 mm.
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d
1mm.
e
1mm.

Fig. 3.

of the peduncle is equal in length to the sum of the other two segments ; the statocyst is conspicuous but without any statolith.

The details of the *antennal peduncle* are shown in Fig. 2*a* in dorsal and in Fig. 3*b* in ventrolateral aspects. The spatulate apex of the long flagellum is represented in Fig. 3*a*, the shaded terminal segments being, in the preserved specimen, brown in colour.

The *eyes* are large and conspicuous, extending as far as the anterolateral spinose angles of the carapace.

The *external maxillipeds* are widely separated basally ; when extended they reach the anterior margin of the antennular somite ; a minute trace of an exopodite is present. The mouthparts were not dissected and examined in detail as I did not wish to damage the specimen. But they appear to be very similar to those of a Puerulus from the Marquesas represented in Fig. 6*a–e* except that the exopodite on maxilliped 2 is rather shorter, being about three-fourths of the merus. The mandibular palp is clearly seen without dissection.

Pereiopod I is appreciably shorter and somewhat more robust than the succeeding limb (Fig. 7*c*) ; the propodus is not quite three times as long as wide and the ratio of dactylus to propodus is 1 : 1·25 ; the merus is rather longer than carpus and propodus. Pereiopods II, III and IV are very similar in size and form, the propodus in each being almost exactly five times as long as wide ; the ratio of dactylus to propodus is 1 : 1·75–1·70 ; the merus equals propodus and carpus. The shrivelled remnant of the exopodite at the base of pereiopods I—IV is very small and is best seen when the limb (ischium to the tip) is detached, leaving the rudimentary exopodite exposed on the stump. Pereiopod V is the shortest and shows no trace of the exopodite ; the propodus is 5 times as long as wide.

Pleopod 1, that attached to the second abdominal somite, is represented in Fig. 3*e* ; most of the long setae on the exopodite and endopodite are omitted ; the *appendix interna* is long, and bears a subterminal plumose seta and a number of terminal coupling hooks (see enlarged view of apex).

Remarks. Unfortunately the post-larvae of the Palinuridae are seldom complete as to antennae, and this is especially true of those with long flagella. Several Puerulus stages, however, have been figured with the antennal flagellum tapering : e.g., that of *Panulirus argus* (Gurney, 1942, p. 234, fig. 93 ; Schmitt, 1935, p. 173, fig. 36 of the young crawfish), and I have examined the specimen figured by Gurney and find that the apex of the flagellum is as represented in Fig. 2*d* ; that of *P. regius* B. Capello (Schmitt, 1926, p. 43, fig. 67) ; of *P. japonicus* (Nakazawa, 1917, plate, figs. 3, 4, and 5 of the post-Peurulus). In these the antenna does not seem to exceed, if it attains, 1·5 times the body length.

Dr. Holthuis of the Leiden Museum kindly informed me by letter that a Puerulus with a long spatulate antennal flagellum had recently been described by Kubo in a paper written almost entirely in Japanese, but with a short summary in English (first paragraphs, p. 91—Kubo, 1950). As no copy of this paper was available in London, Dr. Holthuis sent me a photostat copy. (Later I received a reprint from the author—see p. 28.) Kubo attributes this Puerulus to *Panulirus* " *versicola* " (Latr.)—presumably a misprint for *versicolor*—and finishes his English abstract as follows : " Some descriptions in regard to the puerulus of *P. versicola* have been given by Ortmann (1894) [error for 1891], Calman (1909), and de Man (1916). But no one has given description on the signal feature of the antennae."

Kubo's Puerulus is certainly very similar to that from Kenya ; his figures are small, and in the photostat copy some of the finer details are lost. The flagellum is just over twice the body length and ends in a spatulate expansion which is " stained with rather deep brown colour (in alcoholic specimens)," and I think his figure shows the brown band about one-third of the way along the flagellum. But I do not think that his Puerulus belongs to the same species as that from East Africa described above. As a rule his specimens have two pairs of spines, one in front of the other, at the anterior end of the lateral carinae and those behind the rostral horns are well formed. The general impression one gets from Kubo's figures is that the antennal and antennular peduncles are more robust than those of the Kenya specimen—more like those of specimens from the Marquesas described below (see p. 29 and Fig. 5*a*, *b*.). Nor do I think that Kubo is right in attributing all his post-larvae to *Panulirus versicolor* (Latr.) ; at any rate those figured do not agree with the specimens from Christmas Island which Dr. Calman (1909, p. 444) referred to that species (see p. 26).

I have found an earlier reference to a Puerulus with a spatulate apex to the antennal flagellum in a paper by W. von Bonde (1930, p. 25). In his specimen the antenna is also about twice the body length. The following extract may be quoted from von Bonde's paper : " NOTE.—Only one of my Puerulus specimens of *Panulirus* has the antennae intact. Each is developed at its distal extremity into a large flattened oar-like structure. Such an antenna has been figured by Richters (12) [error for (13)] in a large Phyllosoma (Ph. longicorne Guér., length 38 mm.)." Richters (1873, pl. xxxi, fig. 3) shows a last stage Phyllosoma with a long antenna, the clavate apex of which is rather wider than that represented in Fig. 2*b* and has no terminal spinose projection. The fragment represented in Fig. 2*b* was found in the jar along with a number of post-larvae and young from the Marquesas (see p. 29).

Thus several species of the genus *Panulirus* possess these spatulate antennae in the post-larval stage. Leach's type specimens of *Phyllosoma clavicorne* were collected in West African waters ; von Bonde's post-larvae, which he referred provisionally to *P. bürgeri* de Haan (= *homarus*), were from the East Coast of South Africa ; others are now known from Japan (Kubo, 1950), Kenya and the Marquesas. As von Bonde did not figure his specimens, I do not know from his description whether the antennules are like those of the Marquesas material (Fig. 5*b*), or more slender as in the Kenya specimen (Fig. 3*c*). But, as they are stated to have two pairs of branchial spines on the carapace they agree in this with the Marquesas Pueruli and it is probable that they are referable to *P. homarus* (L.). In the absence of post-Puerulus stages it is not possible to refer the Kenya specimen to the adult species, since it is not known whether abdominal grooves are present or absent. What can be said with certainty is that it belongs to a species with longer and more slender antennules than either *homarus* or *dasypus* (if the latter is regarded as a distinct species—see p. 35).

b. THE POST-LARVA OF *Panulirus versicolor* (LATR.)

(Fig. 4)

MATERIAL. Christmas Island, Indian Ocean. Dr. C. W. Andrews coll. partly on the reef and partly in crevices in the piles of the pier at Flying Fish Cove, reg. no. 1909.5.19.248–252. Five post-larvae.

(Also several later young crawfish stages, reg. no. 1909.5.19, 243–247).

DESCRIPTIVE NOTE. These specimens have been identified by Calman (1909, p. 444), and his determination is fairly certain since he had older stages, up to 74 mm. in length of body, collected at the same time and place. In none of his specimens is the antennal flagellum complete, but in one it exceeds 2·5 times the body length and yet shows no trace of expansion distally—thus it must be considerably longer than that of either the Kenya specimen described above, or of Kubo's post-larvae referred to " *P. versicola* " (Kubo, 1950, p. 94, fig. 3). De Man (1916, p. 61) says of his specimens " external antennae 3-times as long as the body " ; this I at first regarded as a misprint for " 2-times " (as Kubo may also have done), but Calman's material suggests that de Man's statement may be correct. If de Man's specimens were complete the apex of the flagellum was not spatulate or he would certainly have said so. I have since examined de Man's specimens in the Zoological Museum, Amsterdam. They certainly agree with our Christmas Island material but in none are the antennae now intact.

In all the post-larvae there are only three pairs of spinules on the carapace—one at the anterior end of the lateral carinae (not two, as in the majority of Kubo's specimens), one behind the orbits and one behind the supraorbital spines ; in addition two pairs of incipient spinules are present on the cardiac region. They are thus similar to the specimen from Kenya except that the pair behind the rostral horns is distinct. The antennal peduncle is long and slender, rather like but not identical with that of the Kenya specimen (cf. Figs. 4*a*, *b* and 2*a*, 3*c*, *d*). The basal segment differs in that the portion containing the statocyst is shorter while the distal part is narrow and not expanded apically. A large round statolith is visible within the sac (as in all the post-larvae examined other than the one from Kenya, in which it may not have had time to form after a recent moult). Unfortunately, in all the specimens the antennal peduncle is partially collapsed on the inner surface, but it also is relatively long and slender. The pereiopods have also collapsed in most of the specimens, but in one they are normal and I and III are represented in Fig. 4*c*, at the same magnification as those of the other Pueruli. They are slightly longer than those of the Kenya specimen (Fig. 7*c*), or of the Marquesas material described below (Fig. 7*b*).

NOTE ON THE POST-PUERULUS AND LATER STAGES

As stated by Calman (1909, p. 444), the post-Pueruli are brown in colour, with a conspicuous W-shaped marking of white on the carapace and a transverse narrow white band on each abdominal somite, that on somite 1 on the anterior half, those on somites 2–6 parallel to the posterior margins. No abdominal grooves are present,

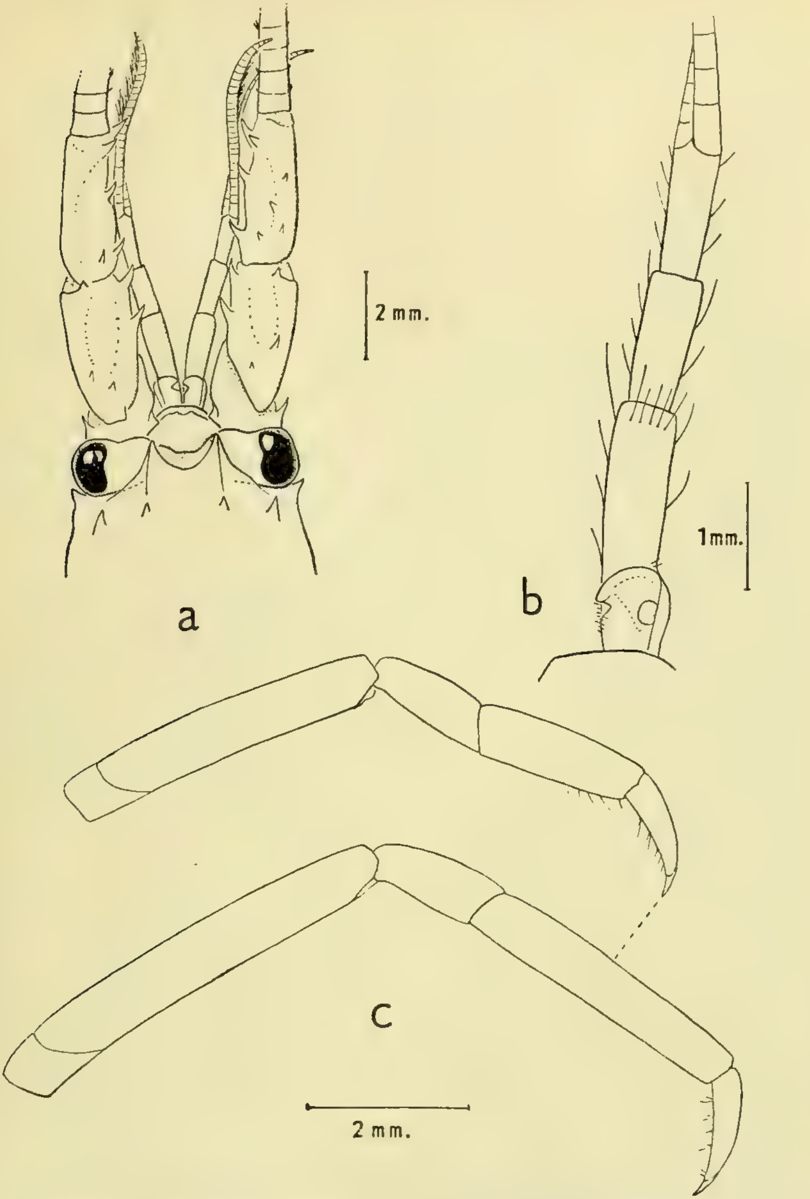

FIG. 4. Puerulus of *Panulirus versicolor* (Latr.) from Christmas Island. *a.* Anterior portion of carapace and antennal and antennular peduncles, in dorsal aspect. *b.* Antennular peduncle in dorsal aspect. *c.* Pereiopod I (upper) and pereiopod III.

as in the adult, but on each somite a number of transverse rows of minute pits, from each of which a short seta emerges, are present. A rather long forwardly directed seta arises from the base of several of the median spines on the carapace. After over 40 years in alcohol the colour pattern of these post-Pueruli is still clear.

In the two older stages from Christmas Island (*c.l.* 25 and 34 mm. respectively) the colour pattern is much nearer that of the adult ; the legs are striped, the dark purplish blotches on the carapace tend to obscure the short median bands of the **W**. The posterior whitish band across each abdominal somite is now flanked anteriorly and posteriorly by a purplish band. What is rather surprising, however, is the presence of a broad but very shallow transverse groove, with slight median interruption, on abdominal somite 2. The pits and setae are now confined to this area, the groove being filled with them while a few continue across the median break. On somite 3 there is a much wider median interruption, beset with sparse setae, between the two setose lateral grooves. On somite 4 there are just two short widely separated lateral patches of setae. Any setae on 5 and 6 are isolated and few in number. These broad shallow grooves on somites 2 and 3, or traces of them, are present in rather larger stages from other localities in the B.M. collection.

REMARKS. As already mentioned on p. 25, I do not think that all Kubo's specimens belong to *P. versicolor* (Latr.). The antennal flagellum in the Puerulus of that species seems to be three times the body length and without a spatulate apex. Since I commenced this paper I have received a reprint from Dr. Kubo and I find that his fig. 4 O shows the **W** pattern rather faintly on the carapace of a young stage (this was not apparent in the photostat copy). I now think that part of Kubo's material only belongs to *P. versicolor*—namely the young with the characteristic pattern and perhaps the Pueruli which he lists with but *one* spine at the anterior end of each lateral carina (Kubo, 1950, p. 93, table 1). The other Pueruli which he figures, with two spines at anterior end of the lateral carina and the stouter antennal and antennular peduncles (Kubo, 1950, figs. 2 and 3) may belong to *P. homarus* (L.) like my specimens from the Marquesas. I do not know how many post-Puerulus and young stages Kubo had. But I assume that in his material no abdominal grooves were present, since that is the case in *P. versicolor*. In the post-Puerulus of *P. homarus* the abdominal grooves are present and show traces of the crenulation as well.

If Kubo's Puerulus with the spatulate antennae really has no abdominal grooves in the next stage, it might be referable to either *P. ornatus* (Fabr.) or *P. polyphagus* (Herbst). The adult of the latter species has a long multi-segmented flagellum on the exopodite of the second maxilliped as represented in Fig. 8*f*, and one would expect a well formed flagellum in the Puerulus also—as in that of *P. inflatus* (Bouvier) represented in Fig. 7*a*. Kubo's Fig. 4 K seems to have no flagellum, or a vestigial one as in fig. 6*d* perhaps. So that *P. polyphagus* would appear to be excluded. On the other hand, *P. ornatus* does not appear to have been recorded from Japanese waters, although it goes as far north as Formosa (Holthuis, 1946, p. 141.).

c. THE POST-LARVA OF *Panulirus homarus* (L.)

(Figs. *2b–d* ; *5a, b* ; 6 ; *7b*)

MATERIAL. (*a*) Marquesas. " St. George " Expedition. W. 38.27.12.24. One Puerulus.

(*b*) Marquesas ; sand of beach, Hana Hevané. C. Crossland coll. 1925–26. Twenty four Pueruli, nine post-Pueruli and young crawfish stages up to 33 mm. in body length.

DESCRIPTIVE NOTES. The 25 Puerulus stages vary in body length from 22 to 24 mm. As each specimen has a narrow band of brown pigment some distance along the antennal flagellum, I thought at first that they must be identical with the specimen from Kenya described above. The antennal flagellum in some specimens shows a hint of expansion of the segments at the broken distal end (Fig. *2c* and *c'*) and the flagellum in these is nearly twice the body length. My suspicion that the apex of the flagellum must be spatulate was confirmed in a rather unexpected way. Lying in the jar amongst detached limbs was the distal end of the antennal flagellum of the last stage Phyllosoma represented in Fig. *2b*. The larval flagellum is unsegmented, but within this can be seen the fully formed flagellum of the Puerulus with the segmentation faintly visible through the chitin. It is obvious that the apex of this flagellum would be spatulate. Presumably this portion of the larval antenna broke off just before or during the critical moult from larva to post-larva. The apex of the larval antenna is very similar to that of the last stage *Phyllosoma clavicorne* Leach, the types of which are in the British Museum collection. The antennal flagellum of these Puerulus stages, therefore, seems to agree with that of the specimen from Kenya.

But on closer examination they were found to differ from the latter in a number of characters. The resemblances are many, chiefly in characters common to nearly all the *Panulirus* post-larvae that have been described such as the presence of the posterior pair of spines on the thoracic sternum. The chief differences are as follows : (i) In all specimens, even the smallest, four pairs of spinules are present on the carapace in addition to the spinose anterolateral angles, namely, a post-ocular pair, a postrostral pair, and two pairs one behind the other at the anterior ends of the lateral carinae. Two pairs of incipient spinules are present on the gastric region as in the Kenya specimen. (ii) The antennules are more robust ; the flagella have some 25 and 23 segments respectively ; the segments of the peduncle are in the ratio of 2 : 1 : 1, as seems usual at this stage, but each segment is broader relatively to its length (cf. Figs. *5b* and *3c, d*). The first segment is 2·5 times as long as wide, the portion containing the statocyst is nearly as long as the distal portion and a conspicuous statolith is always present. In the specimen from Kenya the basal segment is 4 times as long as wide and no statolith was visible. (iii) The antennal peduncle is shorter and more robust. (iv) The pereiopods also seem to be somewhat stouter, especially as regards the merus (cf. Fig. *7b* and *c*). The mouthparts are represented in Fig. *6a–e*.

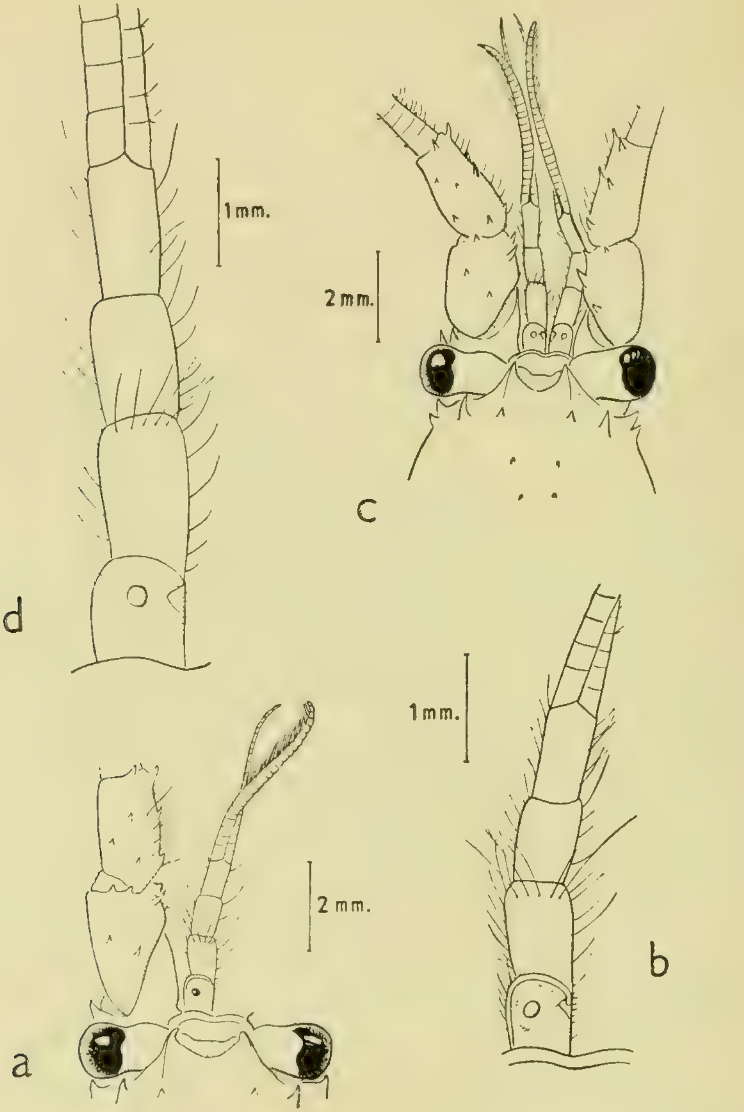

Fig. 5. Puerulus of *Panulirus homarus* (L.) from the Marquesas. *a.* Anterior part of carapace with left antennal and antennular peduncles, in dorsal aspect. *b.* Antennal peduncle. Puerulus of *Panulirus inflatus* (Bouvier) from Coiba. *c.* Anterior part of carapace, antennal and antennular peduncles, in dorsal aspect. *d.* Antennal peduncle.

Remarks. Because several later stages are represented it seems possible to refer these young specimens to the adult species. These young crawfish possess an abdominal groove on each somite, and, moreover, crenulations are present in the older specimens in the lateral portions of each groove. The furrows are slightly interrupted in the centre on the second and subsequent somites. The largest young crawfish measures only 33 mm. from tip of supraorbital spine to tip of telson, but it has a tiny anterodorsal spine on the merus, near the distal articulation, of pereiopods II and III. The soft part of the telson is almost as wide as the hard basal portion ; pereiopod III is longer than pereiopod II by half the length of the dactylus ; the antennular peduncle is now very nearly equal to the antennal peduncle, and the basal segment of the former reaches almost to the distal end of the penultimate segment of the latter. Only one pair of slender spines are present on the antennular tergum at this stage. Many spines are present on the carapace. Holthuis (1946, pp. 110–112) lists the following species as widely distributed in the Indo-Pacific region : *Panulirus dasypus* (Latr.), *P. homarus* (L.), *P. japonicus* (von Siebold), *P. ornatus* (Fabr.), *P. penicillatus* (Oliv.), *P. polyphagus* (Herbst) and *P. versicolor* (Latr.). Of these the species without abdominal grooves or furrows may be excluded, leaving four—*dasypus*, *homarus*, *japonicus* and *penicillatus*. The post-larva of *P. japonicus* has been described by Nakazawa (1917, figs. 3, 4, and 5) ; he figures the antennae of the Puerulus as not exceeding 1·5 times the body length and tapering distally. According to Bouvier (1913, p. 87, key) there are no posterolateral spines on the thoracic sternum in "*Puerulus pellucidus*," which is referred to *P. japonicus*. In any case the antennule of the adult *japonicus* (de Haan, 1833–49, pl. 41/42) has an unusually long slender basal segment to the peduncle, equal in length to the sum of the three segments of the antennal peduncle, and one would expect the specimens from the Marquesas to belong to a species with a relatively short robust antennule. *P. penicillatus* can also be excluded because (i) the margins of the abdominal grooves are never crenulate, and (ii) there is in the adult a short but distinct exopodite on maxilliped 3 so that in the post-larva one would expect the exopodite to be larger than it is in these specimens. As the grooves on the abdominal somites are already distinctly crenulate laterally and slightly interrupted in the median line I have no hesitation in referring these young stages to either *P. homarus* or *P. dasypus*. Most authors are agreed that these two species are very closely related and, in the Appendix, I give reasons for believing that they belong to one rather variable species to which the older name *P. homarus* (L.) should be given.

A short description, without figures, of the Puerulus and post-Puerulus stages of *Panulirus dasypus* from the Red Sea was given by Bouvier (1913, p. 84 ; key to the known Pueruli of the Palinuridae, p. 87). These specimens were found " dans les crevasses du rivage, à Djiboutil " (Bouvier, 1913, p. 88, and 1914, p. 191). These young stages appear to be inhabitants of the littoral zone. The presence of crenulations and slight interruptions on the abdominal grooves at this stages does not necessarily mean that the grooves and sculpturing of the adults will remain of the B-form (or *dasypus* form)—see p. 38.

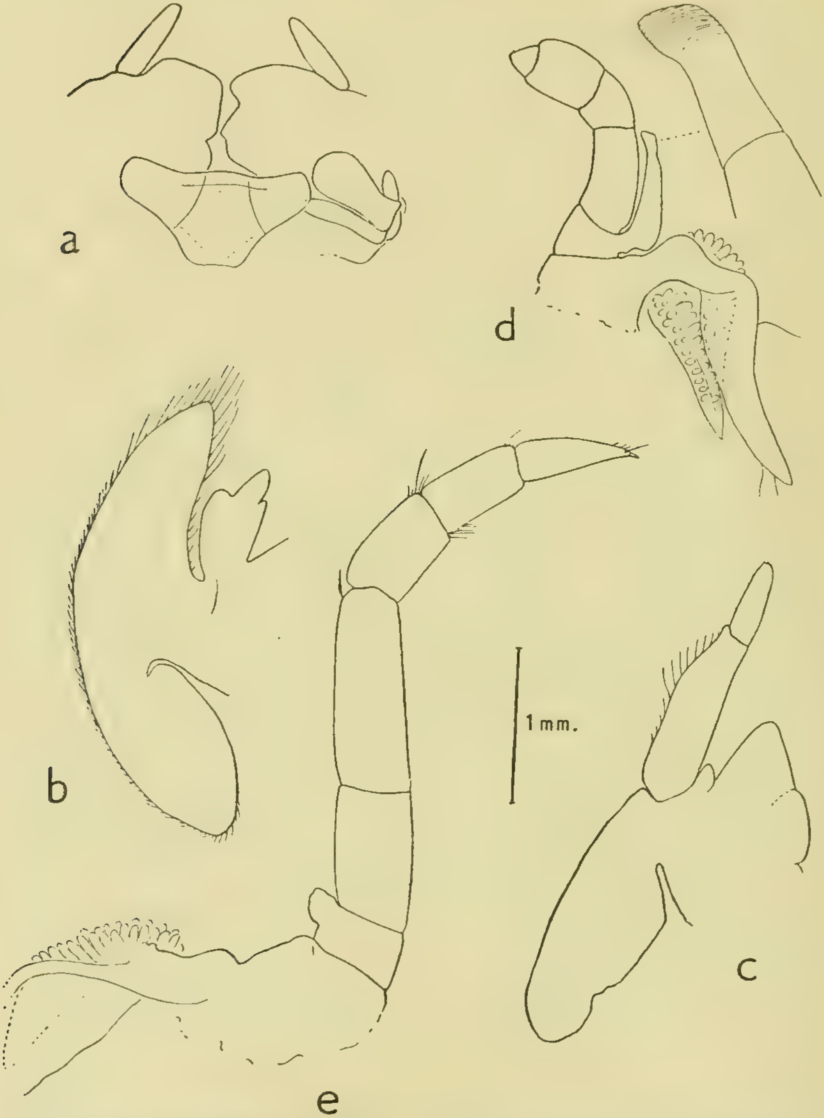

Fig. 6. Puerulus of *Panulirus homarus* (L.) from the Marquesas. *a*. Mandibles, left maxillule and lower lip. *b*. Maxilla. *c*. First maxilliped. *d*. Second maxilliped. *e*. Third maxilliped (distal part of epipodite omitted).

d. THE POST-LARVA OF *Panulirus inflatus* (BOUVIER)

(Figs. 5*c*, *d* ; 7*a*)

MATERIAL. Coiba Island. " St. George " Expedition 1924–25. One specimen measuring 22 mm. in length.

DESCRIPTION. This specimen has the carapace more swollen and distorted than usual. It agrees with most of the Pueruli that I have examined in having a pair of posterolateral spines on the thoracic sternum near the bases of pereiopods V. It differs from all the others in having *two* spines, one immediately behind the other, on each anterolateral angle of the carapace (Fig. 5*c*) and a backwardly directed spine at the posterior end of the median carina, i.e., on the posterior margin of the carapace. In addition to the spinules shown in Fig. 5*c*, namely, at the anterolateral angles, behind the orbits and supraorbital spines respectively, and two very minute pairs on the gastric region, there is only one at the anterior end of each lateral carina.

The antennae are unfortunately incomplete, so that the nature of the apex is unknown ; the longer exceeds 1·5 times the body length and shows no trace of any expansion—which does not necessarily mean that the apex is tapering. The details of the antennular and antennal peduncles are shown in Fig. 5*c* and *d* ; the former is more robust than that of the Puerulus from Kenya, or of the specimens referred to *P. versicolor* (Latr.). They recall those of the post-larvae from the Marquesas described above ; the region of the statocyst is rather opaque but the round statolith is visible. The mouthparts have not been examined in detail, but there is just a vestige of the exopodite on maxilliped 3 (as in Fig. 6*e*). The exopodite of maxilliped 2 has a long flagellum, and in this respect differs from that of the Marquesas material (cf. Fig. 7*a* and 6*d*).

REMARKS. According to Holthuis (1946, pp. 110–111) there are but two species from the Pacific Coast of Central America, namely, *P. inflatus* (Bouvier) and *P. interruptus* (Randall). The latter species possesses in the adult the longest exopodite to maxilliped 3 of all *Panulirus* species and therefore its post-larva should have an even longer exopodite than that of, e.g., *P. argus* (Latr.) figured by Gurney (1942, p. 234, fig. 93E). Since the adult of *P. inflatus* lacks the exopodite on maxilliped 3 and has a large multi-articulate flagellum on the exopodite of maxilliped 2, I have no hesitation in referring this Puerulus to that species.

Amongst the registered post-larvae in the B.M. collection there is another specimen from Esmeraldas, Ecuador (reg. no. 1925.12.8.4), which also belongs to *P. inflatus*. The carapace is normal, and again there is a double spine at each anterolateral angle, but the posterior spine, that at the distal end of the median carina, is lacking. The antennal flagella are incomplete, and there is a rather broad band of brown pigment, a considerable distance from the peduncle, on the left side only. In both specimens there are two rows of 3–4 minute spinules on the proximal half of the soft part of the telson ; no spinules are present in the post-larva from Kenya (Fig. 2*a*) ; in the Pueruli of *P. homarus* there may be two pairs of minute spinules in some of the specimens ; a few spinules are also present in some of the post-larvae of *P. versicolor*.

The holotype of "*Puerulus inermis*" Pocock, said to be the post-larva of *Panulirus guttatus* (Latr.) (Holthuis, 1946, p. 110), has the antennular peduncle of the shorter broader form found in *P. homarus* and *P. inflatus* (Fig. 5*a–d*). The exopodite of maxilliped 2 has a shorter flagellum than that of the Puerulus of *P. inflatus* (Fig. 7*a*) and does not reach beyond the distal third of the carpus of the endopodite. The exopodite of maxilliped 3 is vestigial, as in Fig. 6*e*. The antennal flagellum is

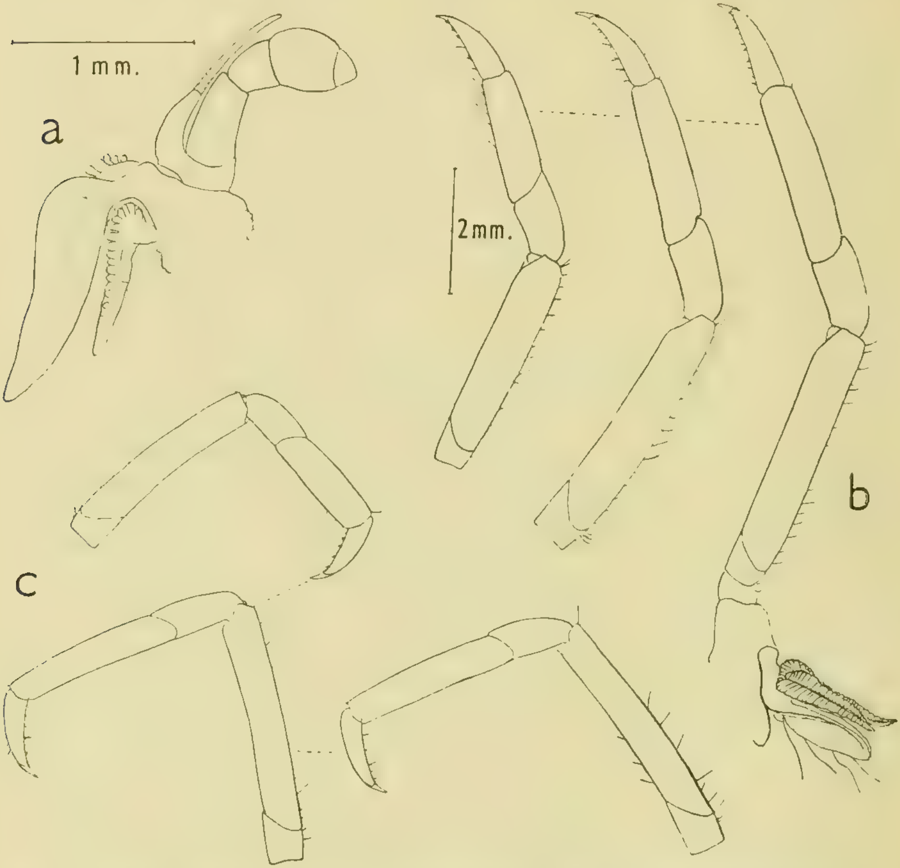

FIG. 7. Puerulus of *Panulirus inflatus* (Bouvier) from Coiba. *a*. Right maxilliped 2. Puerulus of *Panulirus homarus* (L.) from the Marquesas. *b*. Pereiopods I, II and III (from left to right). Puerulus of *Panulirus* sp. from Kenya. *c*. Pereiopods I (above), II and III.

incomplete. Pocock's specimen was dredged in about 10 fms. in Water Bay, Fernando Noronha (Pocock, 1890, p. 516).

APPENDIX

NOTE ON VARIATION OF THE ADULTS OF *Panulirus homarus* (L.)

(Figs. 8 ; 9)

Two Indo-Pacific species of *Panulirus*, namely *P. homarus* (L.)—better known as *P. bürgeri* (de Haan)—and *P. dasypus* (Latreille), are apparently very closely related. The differences between them are indicated in the following extract from Gruvel's key (1911, p. 50) :

> " Exopodite des deuxième maxillipèdes *avec fouet atrophié*. Sillons des tergites abdominaux toujours dentelés et nettement *ininterrompus*
> 4. *P. bürgeri*, de Haan.
>
> " Exopodite des deuxième maxillipèdes *sans fouet*. Sillons des tergites abdominaux dentelés et toujours au moins légèrement interrompus sur la ligne médiane
> 5. *P. dasypus*, Latreille."

Recently Holthuis (1946, pp. 128–136) has attempted to find clear-cut characters by which the two species may be separated ; he lists only some minor differences, and sums up by saying that more abundant material may perhaps show that the two are identical. In recent years I have had considerable correspondence with Dr. Leakey, of the Coryndon Museum, Nairobi, relating to the East African species, and from time to time he has sent me a few specimens for determination. Some of these seemed to agree with *P. homarus*, others with *P. dasypus* as far as the abdominal grooves were concerned, but, as Dr. Leakey pointed out, not always as regards the second maxilliped. For example, two specimens with the deep crenulation and uninterrupted furrows typical of *P. homarus* differed as to the exopodite of maxilliped 2 ; in one a small one-segmented flagellum was present as in Fig. 8*d*, whereas in the other the flagellum was absent as in Fig. 8*c*. The former therefore agreed with Gruvel's definition of *P. bürgeri* (avec fouet atrophié), while the latter agreed with that of *P. dasypus* (sans fouet). Two other specimens with the crenulation much less marked, especially mid dorsally, differed as follows : one was of a reddish colour, with uninterrupted grooves and no flagellum on the exopodite of maxilliped 2 (as in Fig. 8*c*) ; the other was bluish green, with a short but distinct median interruption of the groove on somites 2, 3 and 4 respectively, whereas the exopodite of maxilliped 2 has a large flagellum. (In 1948 I did not observe that the flagellum differed on right and left sides : that on the right is represented in Fig. 8*a* ; the flagellum can scarcely be described as " atrophié," being half the length of the basal segment of the exopodite and rather irregularly segmented ; that on the left is as represented in Fig. 8*d* and " atrophié.")

I have now re-examined the spirit specimens in the British Museum collection that have been referred to *P. bürgeri* (de Haan) and *P. dasypus* (Latreille) by Dr. Calman, who revised the material of *Panulirus* at one time (unpublished), and by

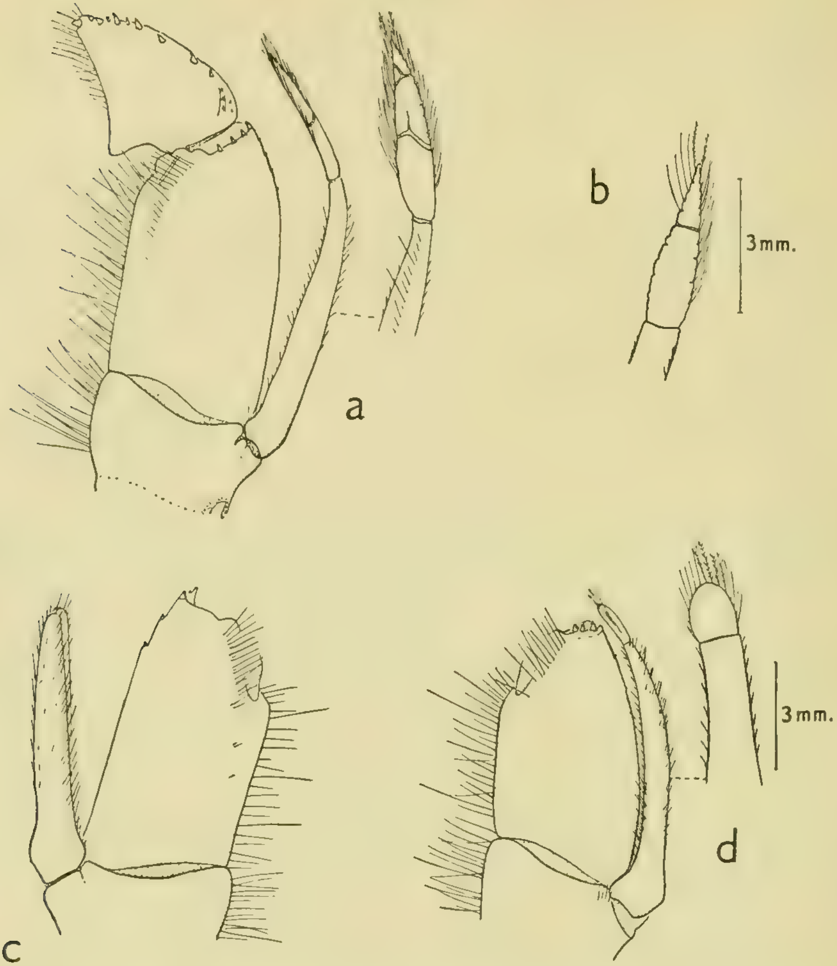

FIG. 8. Portions of the second maxilliped, in anterior aspect, to show the exopodite in various species of *Panulirus*. *a–f*. Adults, *g* and *h* very young specimens.

Panulirus homarus (L.). *a*. From specimen no. 3 in Table, with distal part of exopodite from the side normally facing the endopodite. *b*. Distal part of exopodite of right maxilliped of specimen no. 9. *c*. Left maxilliped of specimen no. 4. *d*. From specimen no. 6. *e*. From specimen no. 1. *g*. Right maxilliped of largest young stage from the Marquesas (*c.l.* = 13 mm.).

Panulirus polyphagus (Herbst). *f*. Left maxilliped of a ♀ (*c.l.* = 66 mm.) with the flagellum, in inner aspect, more enlarged.

Panulirus versicolor (Latr.). *h*. Right maxilliped of a young specimen (*c.l.* = 25 mm.) from Christmas Island.

myself. Unfortunately there are only fifteen specimens, three of which were referred by Dr. Calman to *dasypus* and eight to *bürgeri*, the remaining four being those already mentioned from East Africa. Table I shows briefly the variation in (*a*) the abdominal grooves and the sculpturing in their vicinity, and (*b*) the exopodite

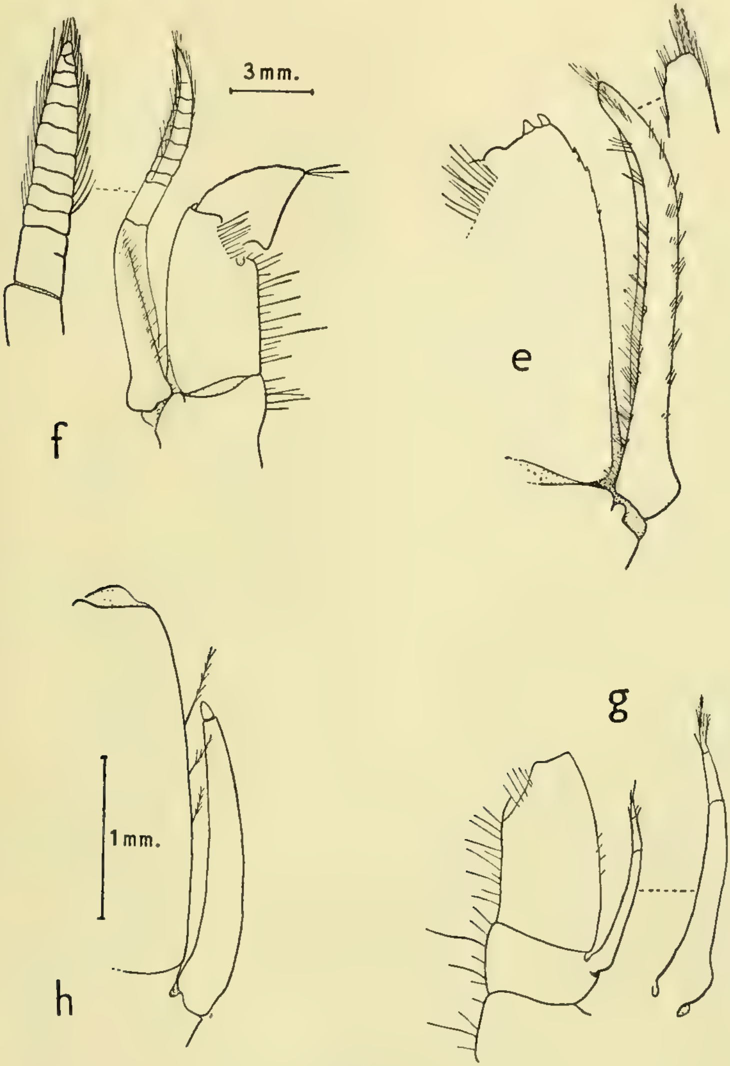

Fig. 8—*e*–*h*.

of the second maxilliped, exhibited by the twelve specimens which obviously belong to the *bürgeri-dasypus* complex. At first I thought that the six specimens with the

TABLE I

Panulirus homarus (= *bürgeri*)—specimens in B.M. Collection.[1]

No.	Sex	*c.l.* in mm.	Reg. no. Locality	Abdominal grooves and sculpturing	Exopodite of second maxilliped		
					Flagellum	Form of flagellum	
1	♂	105	1906.5.29.36	A ++	Absent	R.	Fig. 8*e*.
			Socotra			L	As in Fig. 8*e*.
2	♂	*c.* 90	1948.3.12.1	B +	,,	R.	Alike—as in Fig. 8*c*.
			E. Africa			L.	
3	♂	*c.* 88	1948.3.12.2	B +	Present	R.	Fig. 8*a*.
			E. Africa	2, 3, 4	(dissimilar)	L.	As in Fig. 8*d*.
4	♂	88	Kenya, 1950	A +	Absent	R.	Alike—as in Fig. 8*c*.
						L.	
5	♂	81	1925.8.18.87	A	,,	R.	Ditto.
			Off Natal			L.	
6	♀	80	Kenya, 1950	A +	Present	R.	Fig. 8*d*.
					(similar)	L.	As in Fig. 8*d*.
7	♀	75	28/xi/08	B +	Present	R.	Fig. 9*a*.
	ovig.		No data	2, 3	(dissimilar)	L.	Fig. 9*a*′.
8	♀	61	1925.8.18.86	A +		R.	As in Fig. 8*e*.
	juv.		Off Natal		Absent	L.	Like R, but slightly shorter.
9	♀	60	1910.3.29.36	B	Present	R.	Fig. 8*b*.
	juv.		Goram Id.	2, 3	(similar)	L.	As in Fig. 8*b*.
10	♀	57	1928.12.1.36	A	Absent	R.	Alike—as in Fig. 8*c*.
	juv.		S. Africa			L.	
11	♂	50	80.6	B	Present	R.	Alike—as in Fig. 8*d*.
	juv.		Amboina		(similar)	L.	
12	♂	38	820*a*	B −	R. absent	R.	As in Fig. 8*c*.
	juv.		Ceylon	3, 4	L. present	L.	As in Fig. 8*d*.

A ++. Crenulation and sculpturing very pronounced, of the "*megasculpta*" form.

A +. Intermediate between A and A ++ ; some additional sculpturing and crenulation on certain somites.

A. Crenulation well marked along entire anterior margin of each uninterrupted groove.

B. Crenulation moderately developed, most marked laterally, on anterior margin of groove.

B +. As for B, but with traces of pitting on somites 2 and 3, or 2–4.

B −. Crenulation faintly indicated laterally, fading out medially. Some specimens of the B-form show a slight median interruption of the grooves on the somites indicated below B.

R and L = right and left second maxilliped respectively.

c. l. is measured from tip of supraorbital spine to posterior margin ; in specimens 2 and 3 the supraorbital spines are damaged.

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[1] Recently, in the Zoological Museums of Leiden and Amsterdam, I have examined the material referred to *P. homarus* and *P. dasypus*, and find that it is just as variable as regards mouthparts and abdominal grooves as the B.M. material.

A-form of grooves and sculpturing belonged to *bürgeri*, the other six with grooves and sculpturing of the B-form to *dasypus*. In five of the former the flagellum of maxilliped 2 is absent, whereas in five of the latter it is present on both sides or (in one instance) on one side only. But the fact that in three out of the twelve specimens the exopodites are *dissimilar* on right and left maxillipeds (nos. 3, 7 and 12), and that the three forms of exopodite are thus combined (flagellum present and either long and 2- to 3-segmented, or short and 1-segmented, or absent), proves that this distinction is untenable. I am forced to conclude that these twelve specimens belong to a single variable species, *P. bürgeri* (de Haan), which according to Holthuis must now be called *P. homarus* (L.). In all probability many, if not all, of the references to *P. dasypus* in the literature refer to the less crenulate form of *P. homarus* (this difference does not depend on size as far as one can see). Specimen no. 1 in the Table, from Socotra, is that referred to as *P. dasypus* in Pocock, 1903, p. 214 ; the sculpturing on the abdomen is very pronounced and of the "*megasculpta*" form and I have no hesitation in referring it to *bürgeri*. The exopodite of maxilliped 2 is as long as the merus and yet there is no trace of a suture near the apex (Fig. 8*e*) ; Monod & Petit (1929, fig. 3E) figure the exopodite as only half the length of the merus in their *P. dasypus*, so that the range of variation here is considerable. As this is the largest specimen, the spines on the carapace are rather worn, but they are not as few in number as in Gruvel's specimen of *dasypus* (1911, pl. ii, fig. 5). The anterodorsal spine on the merus of pereiopods II and III, with one exception, have almost entirely vanished, so I do not think that the presence or absence of these spines is of specific importance.

Another difference listed by Holthuis (1946, p. 135), namely that pereiopods II and III are about equal in *homarus* whereas III is appreciably the longer in *dasypus*, is, I think, capable of another explanation. In small specimens of *P. homarus*, irrespective of sex, the pereiopods are relatively short. In the juvenile from Goram Island, for example, pereiopod I reaches the distal end of the second segment of the antennal peduncle, II is just a trifle longer and III a trifle longer still, reaching the distal end of the third segment of the peduncle ; IV reaches the middle of the propodus of I. By the time the carapace has increased to 88 mm. in length (no. 3 in Table) all the legs are a little longer relatively to the antennal peduncle, but the difference between II and III is not marked ; I exceeds the second segment of the peduncle by its dactylus, while III exceeds I by rather more than its dactylus (by 24 mm.) and IV is now a trifle longer than I. In the largest specimen (no. 1) pereiopods I and IV are subequal and reach the distal end of segment 3 of the peduncle much as before, but II exceeds I by the dactylus and one-fourth of the propodus (33 mm.), while III, now clearly the longest, exceeds II by its dactylus (30 mm.) and I by 63 mm. This specimen thus exhibits the commencement of a feature peculiar to senile males at least. The difference gets more pronounced with age, and this may well account for the long third pereiopod in Gruvel's specimen of *P. dasypus* (1911, pl. ii, fig. 5). Gruvel does not mention the sex of the specimen in the legend to the figure, which is one-fourth natural size, giving a *c.l.* of about 200 mm. Recently, when I had occasion to name some large dried specimens for the Zanzibar Museum, I was much impressed by an extraordinary case of allometric growth of pereiopods II and III in senile males of *Panulirus ornatus* (Fabr.). Perhaps the females also exhibit the same phenomenon in old age, but the specimens at my disposal happened to be males. Two that are now in the B.M. collection show the commencement of the differential rate of growth of pereiopods II and III, and a much later stage, respectively. In the smaller the *c.l.* is 134 mm.

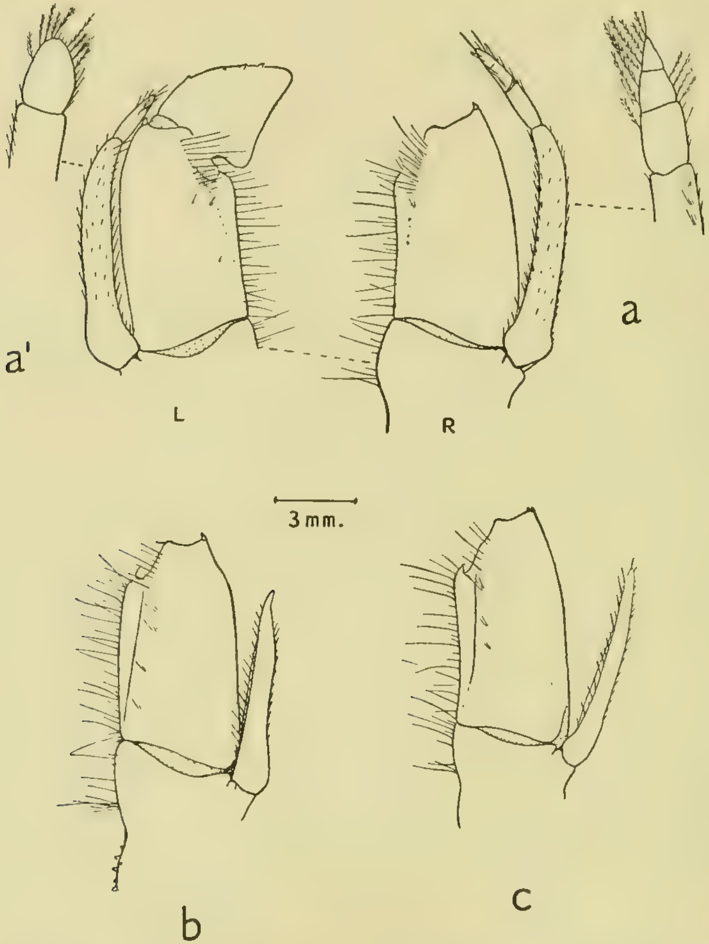

FIG. 9. *Panulirus homarus* (L.). *a* and *a'*. Right and left maxilliped 2 of specimen no. 7 in Table.

Panulirus ornatus ? (Fabr.). *b*. Right maxilliped of ♀ from Shanghai (*c.l.* = 76 mm., reg. no. 62.95). *c*. Same of ♀ from Swatow (*c.l.* = 72 mm., reg. no. 84.2).

and greatest *c.b.* is 85 mm.; pereiopods I and IV are of equal length and probably scarcely reach beyond the distal end of the second segment of the antennal peduncle[1]; pereiopod II exceeds I by rather more than the dactylus (32 mm.); pereiopod III exceeds I by the dactylus and some two-fifths of the propodus (55 mm.). The larger male with *c.l.* 170 mm. and greatest *c.b.* 130 mm. must have been about twice the live weight of the smaller one. Pereiopods I and IV are still equal and relatively short; pereiopod II exceeds I by nearly all its propodus and the dactylus (about 115 mm.), while III exceeds I by some 186 mm.

Perhaps all species of the genus *Panulirus* will prove to undergo the same striking increase in length of some of the pereiopods in old age.

A well-developed exopodite, with long multiarticulate flagellum, on the second maxilliped is characteristic of some species, e.g., *Panulirus polyphagus* (Herbst)—unless, on re-examination of many specimens, the flagellum proves to be variable. This type of exopodite is presumably primitive, and there has been a tendency to reduction and loss of the flagellum within the genus. *P. homarus* would appear to be in process of losing the flagellum, which would explain the variation exhibited by the few specimens available. There are some dried specimens in the collection, but they are not suitable for a study of the mouthparts.

Finally, to return to the three specimens determined as *P. dasypus* by Dr. Calman, I am rather at a loss to know what to call them. They comprise two females from Shanghai and Swatow, China (*c.l.* 76 and 72 mm. respectively), and a young female from Palau Satang. In the juvenile the mouthparts are damaged; the older specimens agree in having the exopodite of the second maxilliped shorter than the merus of the endopodite, and more slender than that of *P. homarus* (Fig. 9*b*, *c*; c.f., Fig. 8*c*). The carapace is quite spiny and, in all three, abdominal grooves are present on somites 2 and 3, absent or evanescent on the posterior somites. There may be a median break or interruption, but the grooves are wider and shallower than in any of the *homarus* specimens examined, and filled with a fine short pubescence. When this is rubbed off one might overlook the grooves entirely and place the specimens in the subdivision without abdominal grooves. There is no trace of the crenulation which is always referred to in connection with *P. dasypus* and the antennular peduncle is relatively longer and more slender than in any of the specimens tabulated under *P. homarus*. These three specimens do not seem to agree with those referred to *dasypus* by Gruvel (1911, pl. ii, fig. 5), Monod & Petit (1929, p. 277, fig. 3 A–E) and others, and which appear to be the B-form of the variable *P. homarus* discussed above. Young specimens of *P. versicolor* have a broad shallow groove, filled with pubescence and with a median interruption, on somites 2 and 3, and just a trace of the setae on each side of somite 4 (see p. 28). These three specimens may belong to another species with abdominal grooves absent, as a rule, in adults—such as *P. ornatus* (Fabr.). Incidentally, there are records of *P. ornatus* from Swatow and Poeloe Satang, which is doubtless the same as Palau Satang—see Holthuis, 1946, p. 141. *P. ornatus* attains a very large size and might retain a juvenile character like these very shallow grooves for a considerable time.

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[1] The pereiopods are all directed forwards and close together, while the antennae are bent back, as convenient for storing dried material, so that exact comparison is not possible.

1 MAR 1955

These specimens are faded, but in the larger ones there are traces of the broad band of colour present on each abdominal somite of large specimens of *P. ornatus*.

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Pp. 43-65 ; 13 *Text-figures*

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ON *SIRPUS*, A GENUS OF PIGMY CANCROID CRABS

By ISABELLA GORDON, D.Sc., Ph.D.

SYNOPSIS

The paper contains an emended diagnosis of the genus *Sirpus* Gordon, a fuller description of the type species *S. zariquieyi* from Spain, and a description of a new species, *S. monodi*, from West Africa. Both species are of very small size, though some of the specimens are sexually mature. The affinities of the genus are discussed ; while it bears some resemblance to *Trachycarcinus* Faxon, it seems to be much nearer to *Pirimela* Leach and is referred provisionally to the family Pirimelidae.

INTRODUCTION

In September, 1947, I received from Dr. Ricardo Zariquiey Alvarez of Barcelona two tiny specimens of what appeared to be a species of Spider Crab from Cadaqués on the north-east coast of Spain. Although the specimens were minute it was obvious that they were females, but I did not at that time observe that the larger one has the genital openings perforate and filled with what appear to be fertilization plugs. Later Dr. Zariquiey sent me a somewhat larger ovigerous female and two males and Dr. H. Boschma of the Leiden Museum lent me a male specimen, all from the same locality. For a time I was much puzzled by this pigmy species of Brachyuran ; while at first sight it seemed to belong to the Oxyrhyncha or Spider Crabs, it proved on closer examination to belong to the Cancroid assemblage, in the wide sense employed by Rathbun, 1930. But its position in that assemblage was not easy to determine, so I consulted Dr. H. Balss, formerly of the Munich Museum, and Dr. Th. Monod of the Institut Français d'Afrique Noire, Dakar. Shortly afterwards Dr. Monod wrote to say that he was sending me some specimens from West Africa that he had found among his undetermined material and which seemed to belong to the same genus. They proved to represent another new species which is described in this paper. Pending the arrival of Monod's specimens I wrote a preliminary paper describing the Mediterranean species under the name of *Sirpus zariquieyi* n.g. and sp., and discussed very briefly the affinities of the genus. Now that a second species is available I am able to give an emended diagnosis of the genus; more figures, a fuller description and details as to habitat of the type species, and a detailed account of my reasons for referring the genus to the family Pirimelidae are also included.

Genus ***Sirpus*** Gordon

Gordon, 1953, p. 304.

Diagnosis (emended). Carapace hexagonal, convex, areolate, the lobes bearing granular clusters or nodules. Front rather narrow, produced, trispinose, the spines or teeth diverging from a common base and thus not in one plane. Orbits large, with forward aspect, shallow and imperfect posteroventrally; two gaps in dorsal margin, a wide one below and one at the inner angle. Eyestalks long, cylindrical, with a bulbous base, retractile within the shallow orbits; eyes deeply pigmented and protected by the postocular or first anterolateral spine. Anterolateral and posterolateral margins about equal, the former with four spines or teeth, the third of which is the smallest. Antennal flagellum long and setose; basal segment (2 + 3) of peduncle but slightly enlarged, not quite filling hiatus at inner angle of orbit but attaining the front, subcylindrical and armed at outer distal angle; segments 4 and 5 subequal. Antennules folded rather obliquely. Anterior margin of buccal cavity distinct. Sternum long and rather narrow. Abdomen rather narrow in both sexes and terminal somite triangular, longer than wide; all seven somites free in female, three to five coalesced in male. No appreciable gap between external maxillipeds; a rounded lobule at antero-internal angle of merus and antero-external angle rounded; antero-internal angle of ischium not produced. Chelipeds equal, carpus and palm of chela nodular and/or granulose. Walking legs rather short, one longitudinal dorsal ridge on carpus, two on propodus; dactyli not compressed but longitudinally ridged, longer than propodus. Male openings coxal; first pleopod a long slender style, about four times as long as the second.

As I explained in the preliminary paper, I have used the less usual spelling of scirpus in deference to the wishes of my botanical colleagues because *Scirpus* is a large and well-known genus or plants. According to Lewis and Short, *A Latin Dictionary*, Oxford, 1917, scirpus, sometimes sirpus, has two meanings: (i) a *rush* or *bulrush*, and (ii) by transference "deriving the idea of intricacy from plaited work of rushes, a *riddle*, *enigma*," and I use it in the latter sense. The gender is masculine.

Two species are known at present, the type species *Sirpus zariquieyi* Gordon from Cadaqués, and *Sirpus monodi* n. sp. from Dakar. The affinities of the genus appear to be with *Pirimela* and *Trachycarcinus*, perhaps nearer to the former—see p. 59–63.

Sirpus zariquieyi Gordon

Gordon, 1953, p. 305.

Diagnosis as for the genus. In this species there is considerable sexual dimorphism, the carapace in the female being distinctly wider and more ovoid than in the male (cf. Figs. 1a, 4 and 5).

Material. From Dr. Zariquiey: (*a*) Two small females collected from fishermen's nets while being cleaned ashore, but from 20 to 40 metres in the neighbourhood of Cadaqués, Provincia de Gerona, Spain. Summer, 1947.

(*b*) One ovigerous female (the holotype) and two small males from *Cystoseira* growth on the rusty iron plates of a sunken ship, in about 20 metres, off Cadaqués, viii.51.

From Leiden Museum: (*c*) One small male, from a fishing net and caught in the vicinity of Cadaqués, 4th–16th August, 1949.

Dr. Zariquiey has very kindly presented the holotype and one male specimen to the British Museum Collection.

DESCRIPTION OF OVIGEROUS FEMALE. This specimen, the largest at my disposal, measures almost exactly 5 mm. from posterior margin of carapace to apex of rostrum and 7·1 mm. in greatest width (between the last pair of anterolateral spines).

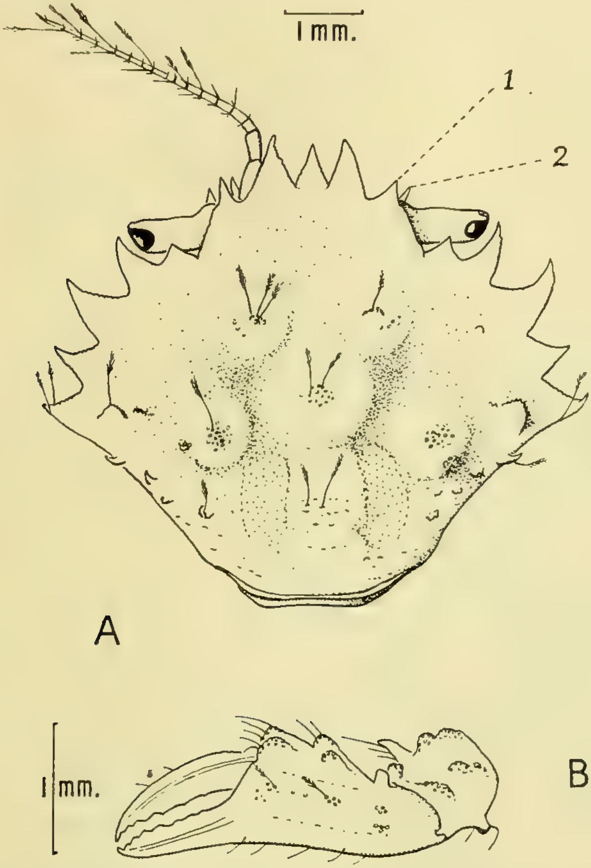

FIG. 1. *Sirpus zariquieyi* Gordon. A. Holotype, an ovigerous female, in dorsal aspect, pereiopods and right antenna omitted. B. Left chela and carpus of holotype. 1. Supraorbital spine. 2. Infraorbital spine.

The form of the *carapace* is represented in dorsal aspect in Fig. 1A. The front consists of three subequal spines ; the median one, or rostrum, is directed obliquely downwards, while the lateral ones are directed forwards and are slightly upturned apically. The *orbits* are wide, so that the distance between the postocular spines (first pair of anterolateral spines, Fig. 1A) exceeds two-thirds of the maximum carapace width. Each orbit is well formed anteriorly but is shallow and incomplete ventro-posteriorly, so that the retracted eye is protected only by the postocular spine. The supraorbital and infraorbital angles are each produced to form a short triangular spine (Fig. 1A, *1* and *2* respectively). The dorsal orbital margin slopes obliquely backwards and outwards to meet the base of a wide triangular spine intercalated between it and the postocular spine. Behind the orbit the anterolateral margin comprises three large spinose projections, the anterior of which is the largest. The posterolateral margins are slightly concave and convergent ; the posterior margin bears a high submarginal crest, and is only a trifle wider than the trispinose front.

The dorsal surface of the carapace is distinctly areolated as represented in Fig. 1A, and the apex of each lobe is beset with some granules. The gastric region has three lobes, two protogastric and one mesogastric—the latter followed by a cardiac and a small intestinal lobe. On either side of the cardiac lobe is a dark reniform depression. The branchial region bears a median lobe (slightly behind and external to the mesogastric lobe), a triangular lobule near the base of the posterior anterolateral spine, and two spinules and a few granular rugosities near the posterolateral margin (Fig. 1A). A number of rather long plumose setae are present as indicated in the figure, but others may have been rubbed off. The anterior portion of the carapace is represented in profile in Fig. 2B.

The *antennae* are long and setose ; the ventral spine on the outer distal angle of segment 2 + 3 of the peduncle is visible in dorsal aspect ; the fourth segment is a trifle longer than the fifth (Fig. 1A, see also Fig. 2A). The flagellum is a trifle more robust than I have indicated in the figure and comprises some 14–16 segments, some of which bear long, distally plumose setae.

The *eyestalk* is much swollen basally, cylindrical in the distal two-thirds, the corneal area is terminal.

The *chelipeds* are equal ; the distal segments of the left one are represented in Fig. 1B. As the carapace is wider than in the male, the merus reaches the apex of the third anterolateral spine and only a small portion is visible dorsally—cf. Fig. 4 where more of the merus is visible beyond the anterolateral margin. The spine on the inner border of the carpus is much longer than in the male (which is of smaller size) ; on the anterior margin a blunt lobule articulates with a similar one on the chela ; the distal half of the outer margin is cristate or lobulate and beset with granules ; on the dorsal surface are two inner, and two or three outer clusters of granules. The fingers of the chela are rather longer than the dorsal margin of the palm ; each bears a median crest or ridge ; the cutting edges are in close contact distally, leaving a slight gap proximally. The dorsal margin of the palm bears a large distal and a smaller median granular prominence, and there are two similar prominences a short distance from the actual margin. Below these is a median series of low granular clusters. The *walking legs* or pereiopods II–V are for the most part bent inwards round the mass of ova and I did not attempt to straighten them out, so have omitted them from the figure. The first pair are about as long as the chelipeds. The right pereiopod V is represented in Fig. 3B ; the merus is about two and a half times as long as wide, the carpus bears a low dorsal ridge near which is a distal depression. The propodus, which is as long as the carpus, has two parallel dorsal ridges ; the dactylus is half as long again as the propodus and bears longitudinal ridges ; in none is it compressed.

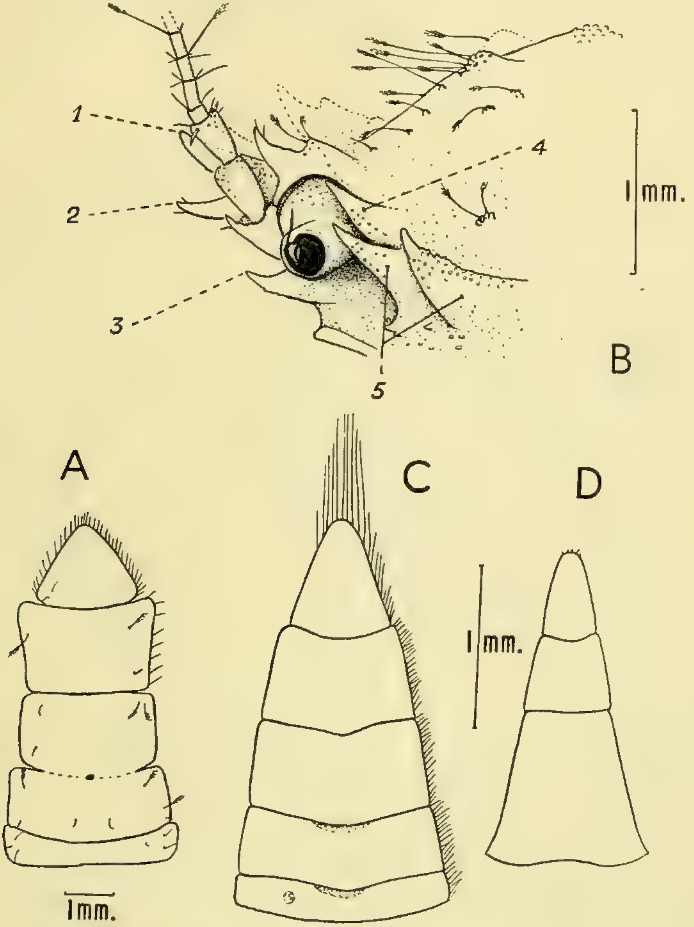

Fig. 2. *Trachycarcinus glaucus* Alc. & And. A. Abdominal somites 3 to 7 of male syntype (*c.l.* = 16·1, *c.b.* = 14·8 mm.)

Sirpus zariquieyi Gordon. B. Left anterior portion of carapace of larger paratype from Lot *a*, in lateral aspect, to show divergence of the frontal spines. C. Abdominal somites 3 to 7 of same specimen. D. Abdominal somites 3 to 7 of male paratype. *1*. Lateral frontal spine. *2*. Median frontal spine. *3*. Infraorbital spine. *4*. Supraorbital spine. *5*. First and second anterolateral spines.

The *antennules* are enclosed in deeper, more developed sockets than in the male represented in Fig. 3A and the crest on the anterior margin of the basal segment of the peduncle is more pronounced. The separation between the base of the rostrum and the epistone is also more pronounced in the female, and the median notch on the anterior margin of the buccal cavity is less distinct. The longitudinal furrow on the ischium of maxilliped 3 is also more pronounced than in the male.

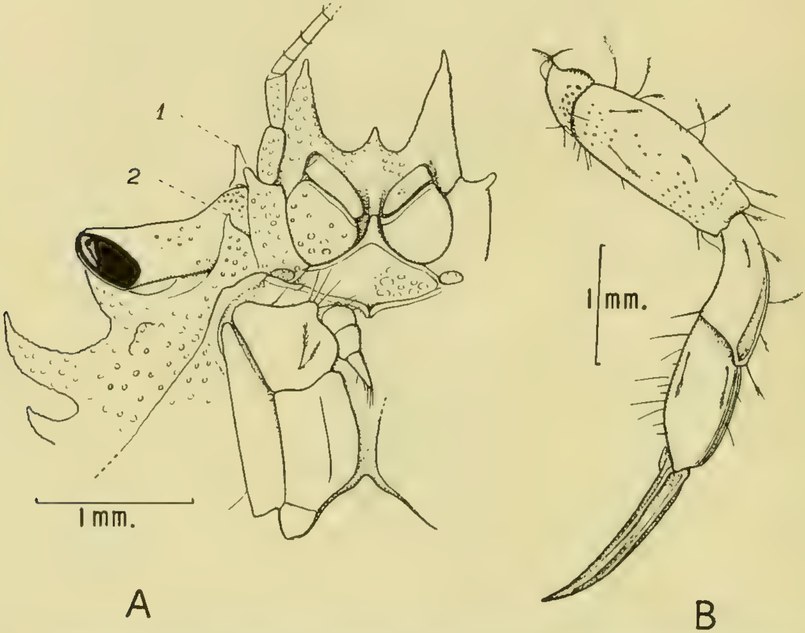

FIG. 3. *Sirpus zariquieyi* Gordon. A. Right anterior portion of carapace of larger male paratype from Lot *b*, in ventral aspect, to show details of orbit, epistome, buccal cavity, etc. B. Right pereiopod V of holotype. *1*. Supraorbital spine. *2*. Infraorbital spine.

All seven segments of the *abdomen* are free ; the first segment is very short and has a transverse granular ridge ; the next three are progressively longer while the last three are of equal length, the terminal one being narrowly triangular with a rounded apex. The abdomen is comparatively narrow, since at its widest it scarcely exceeds the width of the posterior border of the carapace. Somites 3 to 7 are represented in Fig. 2C.

The *ova* are numerous, and measure approximately 0·25 to 0·30 mm. in diameter.

REMARKS. The larger female from Lot *a* measures 4·85 by 5·52 mm. and is very similar to the holotype. It appears to be sexually mature, for the genital openings are distinct and seem to be filled with dark brown fertilization plugs. The clusters of granules on the carapace are more pronounced, and from them arise groups of distally plumose setae. The swollen basal part of the eyestalk is also closely beset with small granules and is separated from the distal portion by a distinct depression. The smaller female from Lot *a* measures 4·00 by 4·81 mm. and is sexually immature; it also is markedly granulose, and the eye-stalk has a depression distal to the bulbous base.

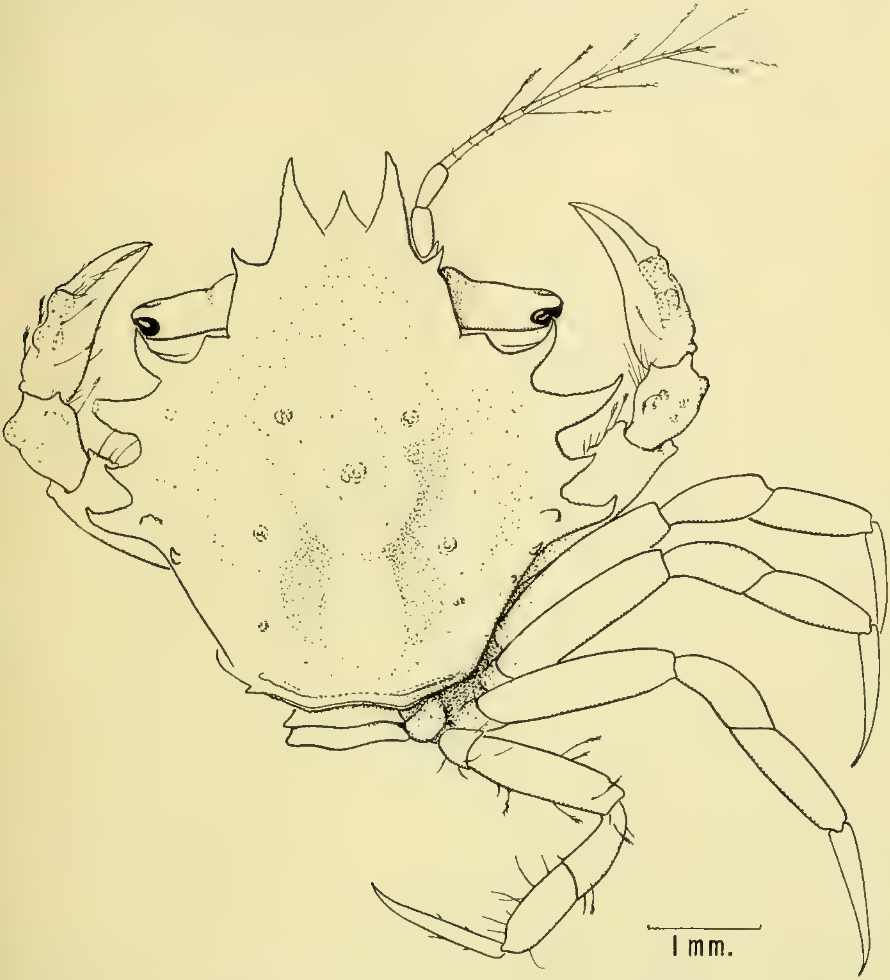

FIG. 4. *Sirpus zariquieyi* Gordon. The larger male paratype from Lot *b*, in dorsal aspect, left antenna and pereiopods II to V omitted.

The *male* paratype from Lot *b* represented in Fig. 4 measures 4·60 by 4·72 mm. It differs appreciably in outline from the female, since the carapace is relatively narrow and the anterolateral spines project but a short distance beyond the orbit. The lateral frontal spines as well as the anterolateral ones are longer and more slender and the intercalated lobe on the orbital margin is less pronounced. The areolation and the granulation of the dorsal surface of the carapace are also less conspicuous. The chelipeds are equal, and the merus projects some distance beyond the anterolateral spines (cf. Figs. 4 and 1A). The spine at the inner angle of the carpus is small; the two pairs of granulose humps on the dorsal border of the palm tend to merge, and the fingers are, as in the female, rather longer than the dorsal palmar margin. The walking legs are more slender than in the female; the merus of pereiopod V is rather more than three times as long as wide, and the ridges on carpus, propodus and dactylus are less distinct. The details of epistome, buccal cavity, orbit, external maxilliped, etc., are shown in Fig. 3A. The abdomen is narrowly triangular; somites 3 to 5 are coalesced, and somite 7 is rather longer than the preceding one (Fig. 2D). The first pleopod, represented in Fig. 6B, is a long slender style reaching almost to the apex of the abdomen; the second pleopod is short, about one-fourth of the first.

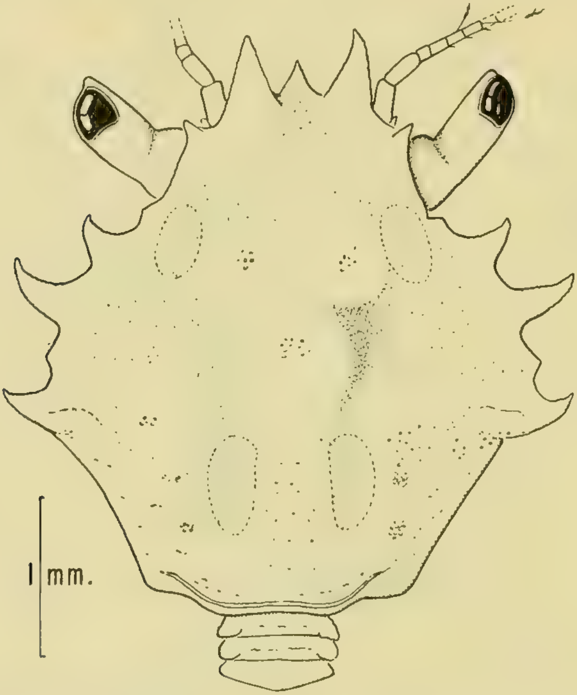

FIG. 5. *Sirpus zariquieyi* Gordon. Carapace of male paratype from Lot *c*, in dorsal aspect.

The specimen received on loan from the Leiden Museum is also a male, and though measuring only 3·42 by 3·58 mm. also has the first pleopod well formed and nearly as long as the abdomen. It differs from the larger male chiefly in that the penultimate anterolateral spine and the intercalated spine of the orbital border are each only incipient (cf. Figs. 5 and 4). The separation of basal and distal portions of the eyestalk is also more marked by the depression mentioned as present in the females from Lot *a*. This specimen has, in addition to the two dark posterior reniform areas, a similar dark patch anteriorly near each orbit. The well-formed pleopods of all these minute males suggests that they may be capable of impregnating females, though they are rather young.

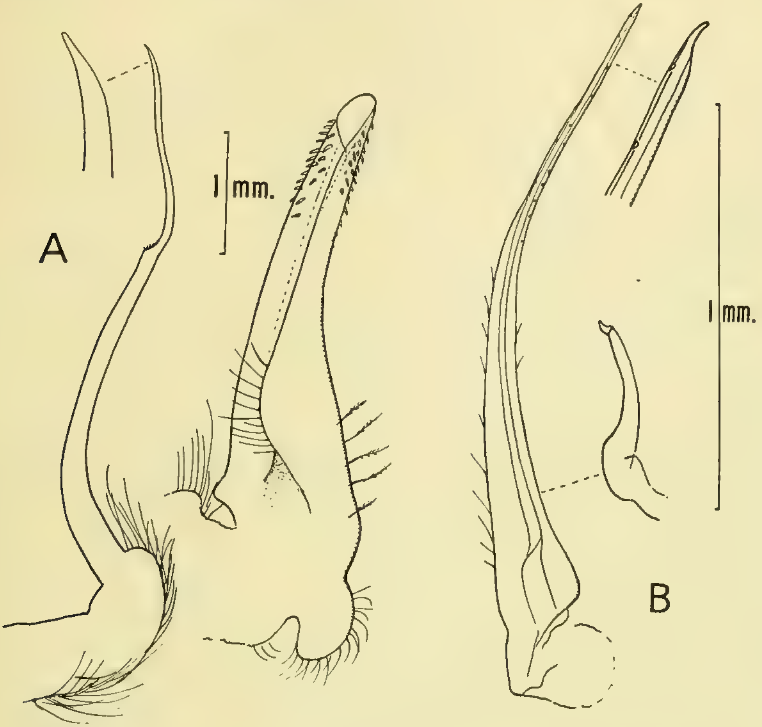

FIG. 6. *Trachycarcinus glaucus* Alc. & And. A. First and second pleopods of male syntype.

Sirpus zariquieyi Gordon. B. First and second pleopods of largest male paratype.

HABITAT. Dr. Zariquiey informs me that the specimens from Lot *b* " were captured a short distance from the coast, at a depth of about twenty metres, amongst long *Cystoseira* algae growing in great quantity on the rusty iron plates of the hulk of a sunken vessel. On examining at home the pieces of rust and algae, I found the

Sirpus at the base of the said algae and on the pieces of rusty iron among other small algae (not determined). In the same place I found hundreds of *Catapaguroides timidus* (Roux), *Thoralus cranchii* (Leach), *Galathea bolivari* Zariquiey, *Porcellana longicornis* (Pennant), *Alpheus dentipes* Guérin and *Synalpheus laevimanus* (Heller)." . . . " The exact point is next to Punta Oliguera facing a sector of the coast called Los Cayals, in the vicinity of Cadaqués (South of Cabo de Creus), Provincia de Gerona, Spain."

Sirpus monodi n. sp.

MATERIAL. (*a*) Collected by M. R. Sourie, at Dakar, 7.iii.1950. See also under habitat p. 57. One ovigerous female, the holotype (*c.l.* = 7 mm., *c.b.* = 7·3 mm.).

(*b*) Collected by MM. Th. Monod and P. Budker on 10.i.41 near Dakar, dredged by the " Cabellou," station 6 bis (" à l'Est de la bouée du Banc de Bel Air, 14° 42′ N., 17° 24′ W.), in about 12 m. Bottom " Sable grossier." One male (*c.l.* = 4·9 mm., *c.b.* = 5·1 mm.).

(*c*) Collected by M. Paraiso at Gorée, near Dakar, on 1.ix.50. Entangled in net used for fishing " langoustes " (*Panulirus regius*) and set in a few metres depth only. One female with genital openings long narrow slits and so probably slightly immature (*c.l.* = 3·9 mm., *c.b.* = 3·8 mm.).

DESCRIPTION OF HOLOTYPE. The *carapace*, represented in dorsal aspect in Fig. 7A, is only a trifle wider than long ; the dorsal surface is markedly nodular in such a manner as to emphasize the areolation. The general outline is hexagonal, with the anterior and posterior margins shorter than the other sides (the orbit being considered along with the anterolateral margin as one side of the hexagon). The front comprises three subequal, bluntly triangular spines, the median one situated below the level of the lateral ones and directed obliquely forwards and downwards. The *orbit* is oblique, rather shallow but well formed anteriorly, imperfect posteroventrally as shown in Fig. 8A, so that the retracted eye is protected only by the postocular spine and the corneal area is visible both dorsally and ventrally. The main lobe of the dorsal orbital margin terminates anteriorly in a blunt supraorbital spine or tooth, and is separated by a narrow hiatus from the blunt lobe intercalated between it and the postocular (or first anterolateral) spine. The ventral margin of the orbit is formed partly by segments 2 + 3 of the antennal peduncle and partly by the lobe bearing the infraorbital spine (Fig. 8A, *2*), behind which it gradually fades out.

The anterolateral margin is divided into four spines, of which the third is the smallest and the anterior is the longest ; the last, though short, is much wider than the third. The posterolateral margins are straight or even a trifle convex, and somewhat convergent. The submarginal crest parallel to the posterior margin is low and interrupted medially.

The two protogastric lobes bear each a blunt, forwardly directed spine or tooth, while the summit of the mesogastric lobe has a prominent wide cluster of granules. On the summit of the cardiac lobe is a pair of granular clusters. A high blunt hump, also beset with granules, is situated near the base of the last anterolateral spine. On either side of the shallow depression separating mesogastric and cardiac lobes is a prominent branchial lobe, with a prominent granular hump on its summit and a smaller one some distance behind this. In addition, there are numerous granular patches or striae on the posterior half of the carapace.

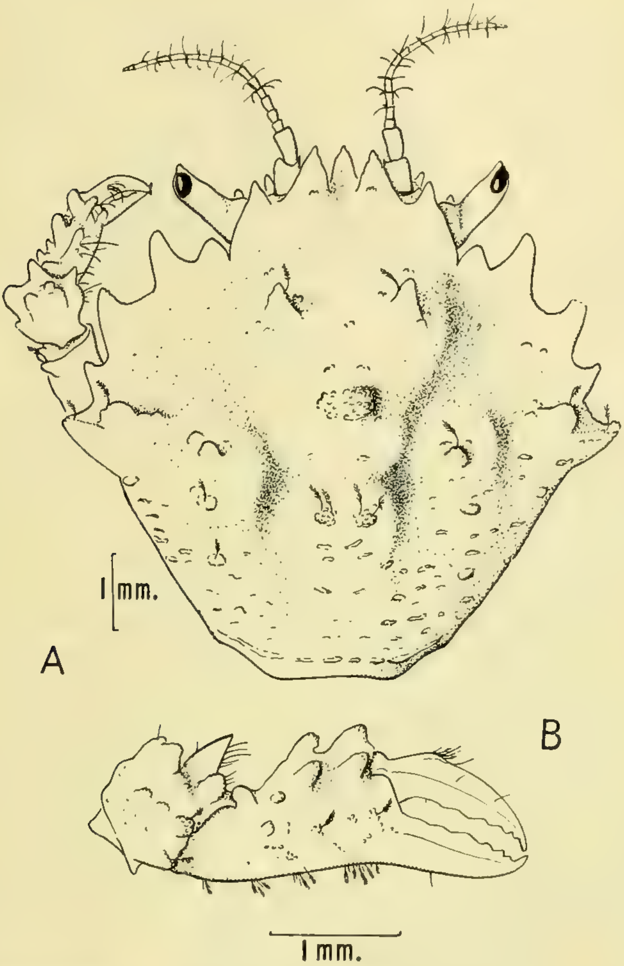

Fig. 7. *Sirpus monodi* n. sp. Holotype, an ovigerous female. A. Carapace and left cheliped, in dorsal aspect. B. Carpus and chela of right cheliped.

The *antennae* are long and setose, but the setae are simple, not pluomse. The blunt spinose anteroventral angle of segments 2 + 3 of the peduncle is visible in dorsal aspect (Figs. 7A and 8A); segments 4 and 5 are of equal length, but the former is the more robust.

The *eyestalk* is swollen and bulbous proximally, slender and cylindrical throughout most of its length ; the distinctly pigmented corneal area is rather small and terminal.

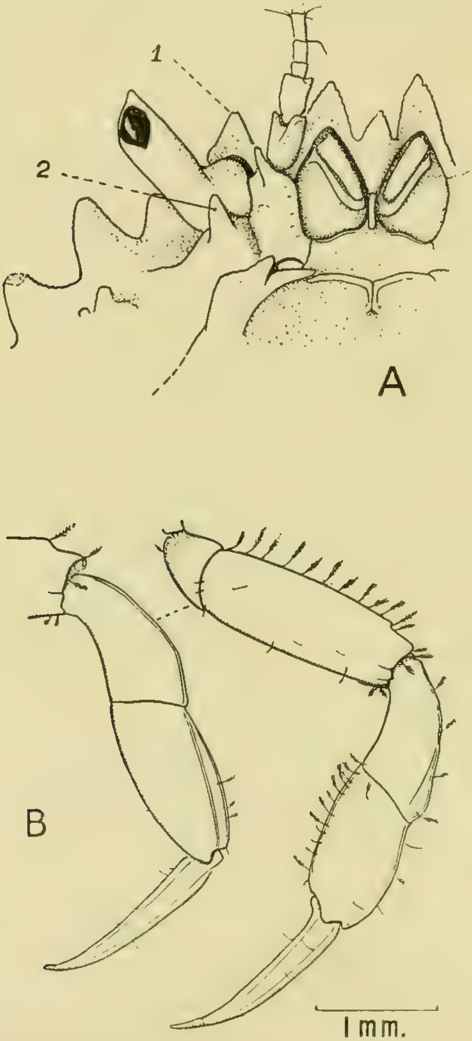

FIG. 8. *Sirpus monodi* n. sp. Holotype. A. Right anterior portion of carapace, in ventral aspect, to show details of orbit, epistome, buccal cavity, etc. B. Pereiopod V and distal segments of pereiopod IV. *1*. Supraorbital spine. *2*. Infra-orbital spine.

The *chelipeds* are equal ; the right, which is detached from the specimen, is represented at a higher magnification in Fig. 7B. Part of the merus is visible in dorsal aspect beyond the two posterior anterolateral spines. The carpus and palm of the chela are both conspicuously nodular ; the fingers are rather longer than the dorsal margin of the palm, and there is a proximal tuft of setae on the upper border of the dactylus, about one-third of the way along. When closed, the cutting edges of the fingers are in contact distally, leaving a narrow proximal gap ; the outer surface of each finger bears a low ridge. The maximum height of the palm is almost equal to the length of the dorsal margin. The spine on the inner border of the carpus is conspicuous.

The *walking legs*, pereiopods II to V, are bent inwards round the large bunch of ova and so have been omitted from Fig. 7A. The distal segments of pereiopod IV are represented in Fig. 8B ; there is a low median dorsal ridge or carina on the carpus, two dorsal ridges on the propodus and several longitudinal ridges on the dactylus, which is not compressed. Pereiopod V is shown also in Fig. 8B ; the merus is not quite three times as long as wide, the dorsal ridge on the carpus is more prominent distally, the propodus is more compressed and the two dorsal ridges are very close together.

The *antennules* are set in deep sockets beneath the front as represented in Fig. 8A ; they are folded obliquely, and there is a conspicuous crest or carina on the swollen basal segment of the peduncle. The *epistome* sends forwards a narrow prominent median carina to meet the backward projection of the front. The anterior margin of the buccal cavity is distinctly marked by a ridge, as shown in Fig. 8A.

All seven somites of the narrow *abdomen* are free ; the maximum width across somites 3 and 4 scarcely exceeds the width of the posterior margin of the carapace. Somites 5 and 7 are equal, and each a trifle longer than somite 6 ; the terminal one is narrowly triangular.

The *ova* are numerous and small (a trifle larger than in the type species).

THE MALE. The single male specimen is represented in dorsal aspect in Fig. 9. Most of the pereiopods are detached from the left side, while the last one, pereiopod V, is missing on the right side. The *carapace* is very similar in outline to that of the female ; the frontal and anterolateral spines are all rather blunt and massive and the supraocular lobe is broad and rounded. As the specimen is younger than the holotype the areolation of the carapace is less pronounced, but the nodular prominences on the principal lobes are distinct. The *eyestalks* are relatively more robust than those of the holotype. The crest near the posterior margin of the carapace is more distinct and continuous. The *abdomen* is rather damaged near its junction with the carapace, as Dr. Monod had dissected out the pleopods from one side and mounted them on a slide, so that my reconstruction of that part may not be quite correct (Fig. 9). Somites 3 to 5 are coalesced ; the distal somites are very similar to those of *S. zariquieyi*, represented in Fig. 2D. The first pleopod is slightly distorted in the micropreparation, but is a long slender style reaching nearly to the apex of the abdomen. It is very similar to that of *S. zariquieyi*, as is the second pleopod. The chelipeds are equal, rather more massive than those of the holotype, although as yet the nodular condition is less highly developed on carpus and palm; the cutting edges of the fingers each bear six well-formed lobes or teeth, the proximal ones being more pronounced than in the older female.

REMARKS. The rather immature female is also very similar to the holotype.

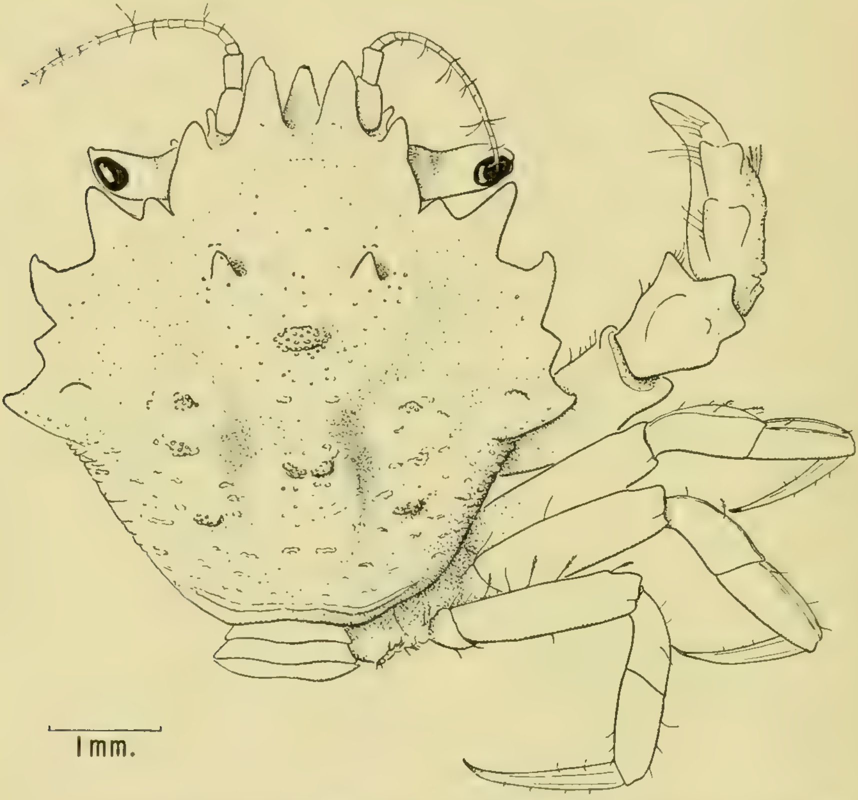

FIG. 9. *Sirpus monodi* n. sp. Male paratype, in dorsal aspect, pereiopods on left side omitted.

This species undoubtedly belongs to the genus *Sirpus* and, like the type species, it reaches sexual maturity at a remarkably small size. *S. monodi* differs from *S. zariquieyi* chiefly in the following respects: (i) It is a much more nodular form, with shorter and much more massive spines on front, orbits and anterolateral borders. (ii) There is no marked difference between the sexes as regards the shape of the carapace. (iii) The chelipeds and walking legs are relatively more robust, and the latter rather shorter as well. The propodus of pereiopod V is rather more compressed. (iv) The setae on the antennal flagellum are simple and rather short, instead of long and distally plumose; the segments of the peduncle are much more robust (cf. Figs. 8A and 3A).

HABITAT. Dr. Monod informs me that the holotype was collected "à marée basse, à Dakar (Anse Bernard) au niveau de l'affleurement de tufs volcaniques (la même station a fourni des *Perimela*[1] *denticulata*). M. Sourie me dit que le petit crabe, très homochrome, étais très difficile à apercevoir sur le sable." Summing up for all three localities he writes: "l'Espèce semble donc, pour le moment être littorale, depuis la zone intercotidale jusqu'à 10–15 m." (letter dated 11.iii.53).

The holotype will be deposited in the Paris Museum, the male paratype in the IFAN at Dakar, and the female paratype in the British Museum Collection.

Since the MS. went to press, Dr. Monod has found an ovigerous female measuring 4·5 by 4·8 mm. amongst some undetermined material in the Paris Museum. The specimen was collected by A. Gruvel on 2.iv.08, at Pointe Cansado, C. Blanco, Morocco, much further north than the type material. It agrees well with the holotype but, being smaller, it has many more granular striations on the dorsal surface of the carapace.

THE SYSTEMATIC POSITION OF THE GENUS

When Dr. Zariquiey first sent me the two small female specimens comprising Lot *a* of *S. zariquieyi* he referred to them in his letter dated 16.ix.47 as "dos Maiidae formas juveniles de sp. ?". On examining them my first impression was that they might be very young stages of *Pirimela denticulata* (Montagu) but this proved not to be the case, and I also was inclined to regard them as young stages of a species of Spider Crab. Now that an ovigerous female is available and I have examined them more carefully, I am convinced that they are not referable to any family of the large subtribe Oxyrhyncha. No Oxyrhynchous crab has the median frontal spine so well formed that the front looks trispinose; when present the median spine or rostrum is minute, and much more ventral in position than the well-developed rostral (or pseudorostral) horns (e.g., in *Maia* or in *Mithrax*). Moreover, in the Oxyrhyncha it is unusual for the anterolateral and posterolateral borders of the carapace to be clearly separated, and the basal segment (or more correctly segments 2 + 3) of the antennal peduncle usually forms a larger part of the lower orbital border. The general form of the carapace in the ovigerous female is distinctly Cancroid, in the wide sense employed by Rathbun, 1930, apart from the front, the median spine of which slopes obliquely downwards and so lies in a different plane from the other two (Figs. 1A and 2B). It would appear that my first impression—that they are closely related to *Pirimela*—was fairly sound. Dr. Balss, who has done so much to elucidate the classification of the Oxyrhyncha and to whom I sent some sketches, writes (6.x.52): "Das Bild einer jugendlichen Krabbe, das Sie mir übersandt haben, gibt nicht eine Oxyrhynche Krabbe, sondern eine primitive Portunide (*Carcinus maenas* ? oder eine verwandte Art)." He was relying entirely on memory, being too ill to go to Munich to consult the literature. Dr. Monod, to whom I also sent sketches and who has since found the specimens belonging to the second species *S. monodi*, writes (9.xii.52): " ne devrait-on pas chercher du côté des Atelecyclidés, aux alentours de *Trachycarcinus* par example ? " Thus all three of us are agreed that the genus belongs to the Cancroid or Cyclometopous Crabs in the wide sense used by Rathbun, 1930.

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[1] According to Monod (1933, *Bull. Com. d'Études hist. sci. Afr. Occ. Fr.* **15**, 2–3: 52) *Pirimela* is etymologically incorrect.

Carcinus maenas or *Carcinides maenas* (L.) is one of the few species of European brachyura the postlarval development of which is known in detail (see, e.g., Shen, 1935, p. 19, text-fig. 20), and the specimens from Cadaqués do not fit into this series. The nearest approach to these specimens that I have discovered so far is a young crab stage referred to *Maia verrucosa* H. M.-Edw. by Cano (1893, Taf. 34, fig. 29), and which I have illustrated (× 2) in Fig. 10A. The size of this specimen is approximately 4 × 4 mm., but I do not think that it can be the first, second or later young crab stage of *M. verrucosa*—Cano did not rear it from the megalopa, of course. Miss Lebour seems to have accepted Cano's interpretation of his specimens, so it is perhaps presumptuous of me to question this stage. The development of *Maia squinado* (Herbst) has been described by Lebour (1927), who obtained the prezoea, first and second zoeae and megalopa from the eggs. But, as she states on p. 797, in no case did the megalopa turn into a crab. The megalopa of *Maia squinado*

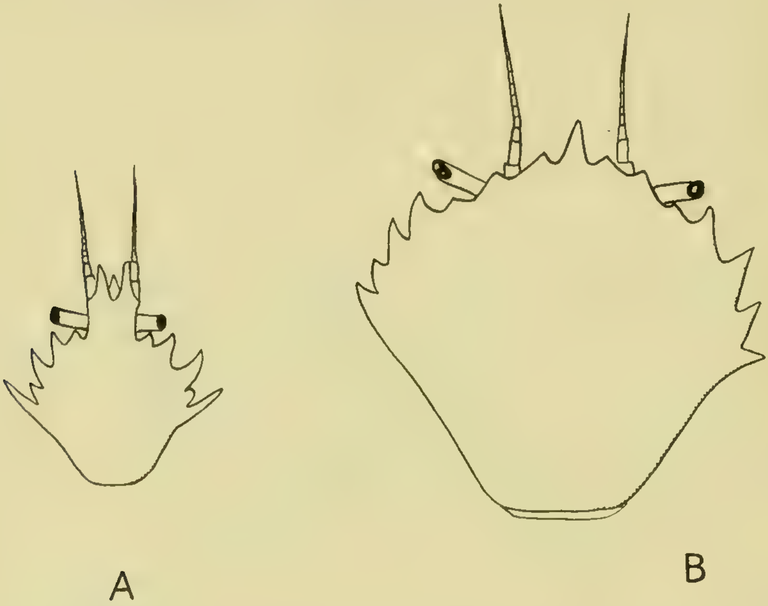

FIG. 10. Two figures after Cano, at twice his magnification.

A. " *Maja verrucosa*, stadio postlarvale " from 1893, taf. 34, fig. 29 (× 8).

B. " Fase adulta (giovane) di *Pirimela* " from 1891, 1892, tav. iv, fig. 4G (Cano's magnification not specified).

from which she obtained the first three young crab stages was obtained from the plankton. What strikes one about these stages is their marked resemblance to young Portunids; although the front is rather more pointed medially, the general resemblance of these young *Maia* to the corresponding stages of several species of *Portunus* and of *Carcinides* is unmistakable (cf. Lebour, 1927, Pl. III, fig. 10 with Lebour, 1928, Pl. VI, figs. 1–3 and pl. 7, figs. 1 and 3). The young crab stages of *Macropodia* and of *Inachus*, on the other hand, are unmistakably Oxyrhynchous (see Lebour, 1927, Pl. 3, figs. 5 and 8). I cannot help wondering whether the megalopa from which these three young stages were obtained is really referable to the genus *Maia.*

To return to Cano's young "*Maja verrucosa,*" it resembles the specimens from Cadaqués as regards the front, eyestalks and orbits, and in the number of anterolateral spines. If the supraorbital spines were omitted from Figs. 4 and 5 and the orbital margins were carried straight back from the bases of the lateral frontal spines, and the anterolateral spines on either side of the smallest one were exaggerated slightly, the result would be much as in Cano's figure (Fig. 10A).

Bouvier (1942) has separated the crabs of " la tribu des ' Corystoidea ' " from the rest of the Brachyrhyncha; to the Corystoidea he has referred the Euryalidae (= Corystidae restr.), Atelecyclidae and Cancridae of Rathbun (1930, pp. 10, 148 and 176) and others, placing the genera in five families (see pp. 47–48 for his scheme). The genus *Trachycarcinus* he places in the family Corystidae, subfamily Atelecyclinae; *Pirimela* in the monotypic family Pirimelidae. I had noted the rather striking resemblance between the males of *Sirpus zariquieyi* and *Trachycarcinus corallinus* Faxon for example. In the British Museum Collection the genus is represented by one male syntype of *T. glaucus* Alcock & Anderson and one male specimen of *T. balssi* Rathbun received from Dr. Sakai of Japan. *Sirpus* agrees with the diagnosis of *Trachycarcinus* given by Rathbun (1930, p. 164) as regards the orbits, which are " large, with forward aspect, imperfect," but it differs in many respects: (i) The eyestalks are retractile within the orbits but they are not " very small," nor are the eyes " dull and faintly pigmented." (ii) The front is wider and, though trispinose, the spines do not lie in one plane as they do in *Trachycarcinus.* (iii) The anterior margin of the buccal cavity is very distinct and the ridges of the endostome are less pronounced than in *T. balssi* for example. The external maxillipeds also differ in the two genera; in *Trachycarcinus* there is a considerable gap between the maxillipeds anteriorly, the anterior inner angle of the ischium is advanced and the merus is " obliquely truncated without emargination at antero-internal angle " (Rathbun, 1930, p. 164, pl. 72, fig. 6)). (iv) The carapace is not pentagonal with long, nearly straight, anterolateral margins, but hexagonal (more ovoid in the female of the type species *S. zariquieyi*). (v) The antennules do not fold longitudinally or lengthwise as in the Atelecyclidae, but obliquely, as shown in Figs. 3A and 8A. (vi) The abdomen of the male is more narrowly triangular, with a longer apical somite and somites 3 to 5 completely coalesced (cf. Figs. 2D with 2A—somites 4 and 5 are imperfectly coalesced in *Trachycarcinus glaucus* and in *T. corallinus* but all seven somites are free in *T. spinulifer*); and, judging from the figure given by Rathbun (1930, pl. 72, fig. 5), that of the female is also narrower, with a much longer apical somite, in *Sirpus*. (vii) The pleopods of the male also differ markedly in the two genera as represented in Fig. 6A and B; in *Trachycarcinus* the first pleopod is relatively straighter, more robust and shorter, while the second pleopod is longer than the first and has a terminal lash. In all the genera of the Atelecyclinae that I have examined, namely *Telmessus*, *Peltarion*, *Atelecyclus*,[1] *Trachycarcinus* and *Pliosoma*, pleopod 2 of the male is as long as or longer than pleopod 1 *except* in *Pliosoma*; in the latter pleopod 2 is very short, measuring only about one-sixth of pleopod 1, and the genus may be referable to a different subfamily. I should expect *Erimacrus* and *Trichopeltarion* to conform to the general pattern (i.e., to have pleopod 2 long), but I have no material at my disposal; Rathbun and Bouvier both omitted to mention the form of the male pleopods. In the Corystidae (or Corystinae of Bouvier) pleopod 2 varies in relative length, being longer than pleopod 1 in *Pseudocorystes* and *Podocactes*, about the same length as pleopod 1 in *Gomeza* and *Jonas*, shorter than, but exceeding half the length of, pleopod 1 in *Corystes*. In the family Bellidae of Bouvier's scheme (Acanthocyclinae in that of Rathbun) pleopod 2 reaches nearly to the apex of pleopod 1 in *Bellia*, but is rather less than half as long as pleopod 1 in *Acanthocyclus*. In the genus *Cancer* pleopod 2 is rather longer than pleopod 1—

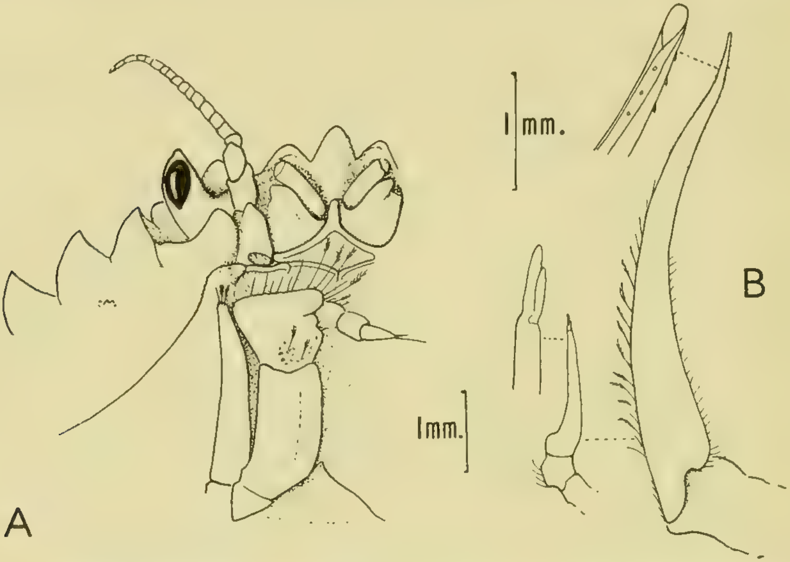

FIG. 11. *Pirimela denticulata* (Montagu). A young male from Jersey (width of carapace approx. 10·7 mm.). A. Part of carapace, in ventral aspect, to show details of orbit, epistome, buccal cavity and third maxilliped, etc. B. First and second pleopods, with apex of each further enlarged, of young male (10·4 × 11·4 mm.).

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[1] Stephensen (1945, p. 222) is in error when he says of the subfamily Atelecyclinae, "Plp. 2 short, of usual shape"; Brocchi, to whom he refers, says on p. 103 that pleopod 2 of *Atelecyclus cruentatus* Desm. is long, and his fig. 199 shows a long slender appendage which exceeds pleopod 1 (figs. 197–8).

family Cancridae of Bouvier's scheme—whereas it is short in *Thia, Kraussia* (family Thiidae) and in *Pirimela* (family Pirimelidae) (see Fig. 11B).

Fig. 12 represents a small male specimen of *Pirimela denticulata* (Montagu) from Jersey in dorsal aspect. The areolation of the carapace is very similar to that found in both species of *Sirpus*. The front is trilobed, the median one being the most prominent, and all lie in the same plane. The antennae are rather long but as a rule are not setose, though a few very short plumose setae may be present in some specimens. The orbit is closed and narrow, but the dorsal border comprises three lobes, separated by two notches ; the eystalks are rather short, but the basal portion is bulbous (Fig. 11A). The anterolateral margin bears five forwardly directed spinose lobes. *Pirimela denticulata* grows to a larger size and is far less precocious than either of the species of *Sirpus*—the first trace of the genital opening appears when the females measure 9 to 10 mm. in maximum width, and the opening is not fully formed until they measure 11 to 12 mm. across the last pair of anterolateral spines. It is not so easy to ascertain when the males reach sexual maturity ; in a

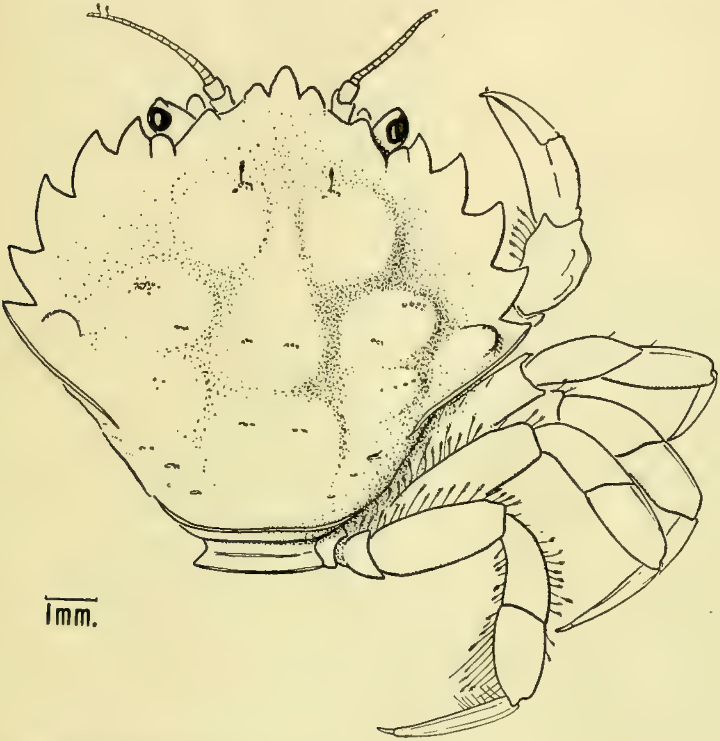

FIG. 12. *Pirimela denticulata* (Montagu). Young male, in dorsal aspect, left pereiopods omitted.

small specimen measuring 7 mm. in width the first pair of pleopods is short and obviously immature, but by the time the carapace measures 8·5 to 9 mm. in width these pleopods are well-developed long styles. *Sirpus* appears more closely related to *Pirimela* than to *Trachycarcinus* in the following respects: (i) The manner in which the antennules are folded, the distinct anterior margin to the buccal cavity, the well-pigmented eyes and the form of the external maxilliped (cf. Figs. 3A and 8A with 11A). (ii) The form of the abdomen in both sexes. (iii) The form and relative lengths of the pleopods of the male (cf. Figs. 6B and 11B). (iv) The lobulation of the carapace—the female of *S. zariquieyi* also approaches more nearly to *Pirimela* in general form of the carapace (cf. Figs. 1A, 7A and 12). (v) The walking legs are also very similar. At present we do not know how large either of the species of

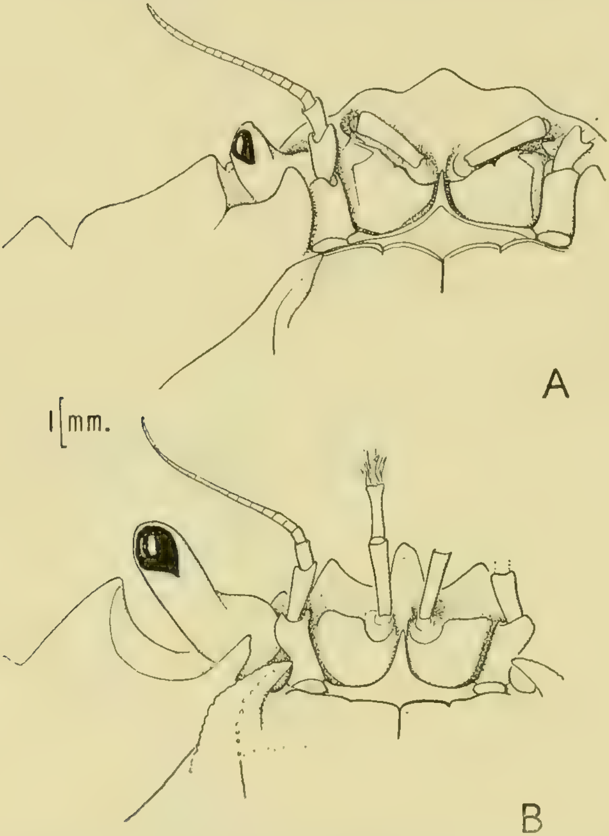

FIG. 13. A. *Portumnus biguttatus* Risso. B. *Portumnus latipes* (Pennant). Anterior portion of carapace, in ventral aspect, to show details of front, orbit and eyestalk, antenna and antennules, epistome and anterior margin of buccal cavity.

Sirpus may become, but they would appear to be really of very small size, since even in the smallest males the pleopods are already well formed, and in all but the smallest female the genital openings are visible. It is unlikely that the females would alter appreciably with increase in size, since in each species the largest bears ova.

Cano (1891, tav. iv, fig. 4G—published in 1892) gives a figure of what he calls the " fasa adulta (giovane) di *Pirimela*," which I have reproduced at twice his magnification in Fig. 10B. As Cano does not appear to give his magnification I do not know the size of his specimen. It differs appreciably from all the stages that I have examined chiefly in having wide shallow orbits, long eyestalks and only four anterolateral spines—in these respects his specimen recalls *S. zariquieyi* even more than *Pirimela*, although the front is nearer to that of the latter (Cano's specimen is represented in his figure as rather asymmetrical). At present the postlarval development of *Pirimela denticulata* is not known ; it seems unlikely that Cano's specimen is a young crab stage of *Pirimela*, but if it is the orbit must alter markedly with age and the number of anterolateral spines increase to five (cf. Figs. 12 and 10A).

The wide shallow orbit alone would not necessarily exclude these new species from Cadaqués and West Africa from the genus *Pirimela*. The two European species of the genus *Portumnus* differ from each other markedly as regards orbit and eyestalk as represented in Fig. 13A and B. In *Portumnus biguttatus*[1] Risso the orbit is closed, narrow, and deep enough to conceal the cornea of the retracted eye dorsally, though not ventrally (owing to the deep gap or hiatus in the ventral margin). The trilobed front is separated by a wide shallow emargination from the low rounded supraorbital lobe. The principal segment (2 + 3) of the antennal peduncle fills the gap between the orbit and the antennular fossa, and, in the specimen from which the figure was made, is slightly movable. In *Portumnus latipes* (Pennant) the front is more markedly three-pronged ; the orbit is wide and shallow, affording no concealment for the cornea of the retracted eye ; moreover, there is a wide gap between the infraorbital spine or angle and the antennal peduncle (Fig. 13B). *Sirpus* and *Pirimela* differ from each other as regards orbit and eyestalk in much the same way as do these two *Portumnus* species. However, *Sirpus* differs sufficiently from *Pirimela* as regards the form of the front, the number and form of the anterolateral spines, the more setose antennae, and in the absence of a " lobe portunien " on the endopodite of the first maxilliped (see Bouvier, 1942, p. 32, fig. 15), to justify the erection of a new genus. But these differences hardly seem sufficient to justify a new family for the reception of *Sirpus*.

Authors do not seem to agree as to the systematic position of the genus *Pirimela*. Pesta (1918, pp. 386–387) places it with *Cancer* and *Carcinides* in the family Cancridae ; most authors place *Carcinides* in the Portunidae. Nobre (1931, p. 84 ; 1936, pp. 48–49) refers it to the Cancridae along with *Cancer* and *Xantho* ! In the Plymouth Marine Fauna, 2nd edition, 1931 the family Cancridae includes *Cancer* and *Atelecyclus*, while *Pirimela* is referred to the monotypic family Pirimelidae. Bouvier (1942, pp. 47–48) includes the Cancridae and the Pirimelidae, each with only the genus from which the family name is derived, in his Corystoidea, which he removes from the Brachyrhyncha (and yet he refers to *Pirimela* as having a narrow "lobe portunien" as mentioned above). Lebour (1944, p. 15) writes: "As far as we know from its larval stages *Pirimela* is probably related to *Portunus* and *Cancer*, perhaps more nearly to *Cancer*." Enough has been said to show that the classification of the Brachyura is in need of thorough revision. In the meantime I am inclined to place *Sirpus* near to *Pirimela* rather than to *Trachycarcinus*, although it shows some resemblance to the latter. In the shape of the abdomen in both sexes and also of the male pleopod 1 it is much nearer to *Pirimela* than to *Carcinides* and the dactylus of pereiopod V is not compressed as in the latter genus, which is a primitive Portunid (see p. 57 for Dr. Balss' view).

---

[1] Referred to the genus *Portumnoides* by Bohn 1902, p. 448.

The two genera of the family Pirimelidae may be distinguished as follows:

A. Front trilobed, the lobes in one plane; orbits narrow and complete; anterolateral margin divided into five teeth; antennal flagellum not obviously setose; specimens reaching a fair size (up to 25–30 mm. across carapace) *Pirimela*, Leach.

B. Front trispinose, the spines not in one plane; orbits wide and incomplete ventroposteriorly; anterolateral margin divided into four teeth or spines of which the third is the smallest; antennal flagellum setose; specimens of very small size . . . . *Sirpus*, Gordon

The study of these small crabs was particularly difficult, I think, because of their extreme sexual precocity, as a result of which they have inevitably retained a number of juvenile characters. For example, the great fronto-orbital width, the projecting front, the relatively large frontal, orbital and anterolateral spines and the long setose antennae are all strongly reminiscent of the first postlarval stage of *Cancer pagurus*, figured by Cunningham (1898, *Proc. zool. Soc. London*, p. 204, pl. xxi, fig. 1). Shen has figured the outline of the carapace of the first nine young crab stages of *Carcinus maenas* (1935, p. 19, fig. 20), so that one can see at a glance how the shape and relative proportions vary with age. As regards size, the largest ovigerous females of the genus *Sirpus* would be equivalent to the sixth young crab stage of *Carcinus* and sexual maturity is reached even at a smaller size. The two species of the genus *Sirpus* may therefore be regarded as neotenous. de Beer (1951, 'Embryos and Ancestors,' revised edition, p. 52), applies the term neoteny to "cases where the adult animal retains larval characters"; where a complicated metamorphosis occurs, however, it is more likely to be the postlarval characters that are retained by the adult.

Acknowledgments.

I wish to thank Dr. Zariquiey of Barcelona, Dr. Boschma of Leiden and Dr. Monod of Dakar for sending me these very interesting specimens for study. I am also grateful to Dr. Balss of Munich and Dr. Monod for giving me their views on the relationship of the genus, and to my colleague Mr. A. C. Townsend for assistance in finding a name for it.

The authorities of the British Museum (Nat. Hist.) are much indebted to Dr. Zariquiey for presenting to their Collection the holotype and a male paratype of *S. zariquieyi*, and to Dr. Monod for presenting the female paratype of *S. monodi*.

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THE *MACROTRITOPUS* PROBLEM

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W. J. REES

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 2 No. 4
LONDON: 1954

THE *MACROTRITOPUS* PROBLEM

BY

W. J. REES, D.Sc.

Pp. 67–100 *; Pl.* 3 *;* 17 *Text-figures*

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THE *MACROTRITOPUS* PROBLEM

By W. J. REES, D.Sc.

SYNOPSIS

The Atlantic species of the larval octopod genus *Macrotritopus* (*M. equivocus*, *M. scorpio*, *M. kempi* and *M. danae*), together with some *Macrotritopus*-like larvae described by Degner (1925), have been re-examined, and the type material of all but the first two species has been available for study. All these forms were found to be growth stages of *Scaeurgus unicirrhus* (Delle Chiaje), an octopus of the continental shelf. The *Macrotritopus* larvae appear to be able to delay settlement if they are swept over very deep water by water movements, and to continue growing to nearly twice the normal size for metamorphosis. These large larvae (found also in other groups of animals) are now termed extended pelagic stages, and their significance in dispersal and in maintaining the homogeneity of populations of widely distributed species is discussed.

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A. INTRODUCTION

This study originated from a desire to carry further earlier work on the planktonic stages of *Octopus vulgaris* (Rees, 1950, 1952). In particular, it was hoped that late planktonic stages of this species could be obtained from a search of plankton hauls made in the tropical Atlantic by the ships of the "Discovery" Investigations. During the course of this work a number of *Macrotritopus* larvae were collected, and it was the remarkable similarity of the youngest *Macrotritopus* larvae to those of *Octopus vulgaris* (except in the very long third arms) which led me to re-examine them in relation to a known adult or adults.

The startling agreement of the chromatophore patterns in *Macrotritopus* and *Octopus vulgaris* suggested some relationship, but further investigations showed conclusively the *Macrotritopus* could not be linked with any littoral species. Final conclusions indicate that all the so-called *Macrotritopus* spp. of the Atlantic belong to one species, and that the adult is *Scaeurgus unicirrhus* (Delle Chiaje), a benthic octopod living at moderate depths near the edge of the continental shelf.

B. THE GENUS *Macrotritopus*

Grimpe (1922) proposed the name *Macrotritopus* as a generic name for a juvenile pelagic octopod, *Octopus gracilis* Verrill, because the third arms greatly exceeded the others in length. Later, Robson (1929*b*, p. 168, *et seq.*) changed Verrill's name to *equivocus* because the name *gracilis* was preoccupied. While recognizing that *Macrotritopus* was only a convenient label for juveniles, whose adult stages might or might not be known, he referred four other forms to it, viz.:

Octopus scorpio (Berry), *Macrotritopus kempi* Robson, *Octopus bandensis* Hoyle and *Octopus elegans* Brock. Of these, *Octopus* (*Macrotritopus*) *equivocus* Robson and the first three above were described from the Atlantic and the Mediterranean. The last two are Indo-Pacific species and need not concern us further here. Later, Joubin & Robson (1929) described *Macrotritopus danae* from the collections of the Danish Dana Expeditions. All the known Atlantic specimens of *Macrotritopus* are juveniles exhibiting no sings of hectocotylization.

It has also been found necessary to reconsider some larvae described by Degner (1925) as *Scaeurgus* (Troschel sp. juv.), because on re-examination they prove to be *Macrotritopus* larvae.

The *Macrotritopus* forms which have been described are so distinctive in appearance that their true identity is masked by larval characteristics. In this connection the views of earlier workers are of interest. Verrill (1884), in considering his own *Octopus gracilis* (i.e., *equivoca*), was " very certain it is not the young of any known species." Robson (1929*b*) was unable to make up his mind about the status of these forms, as is evident from his statement: " We must either conclude that they are the young forms of species hitherto undescribed or that they undergo some kind of metamorphosis in the course of subsequent development, as a result of which they assume the adult form of some described species." More recently, Pickford (1945) in discussing the American forms *M. equivoca* and *M. scorpio*, expressed the opinion that " There is no possibility that these strikingly distinct young animals with their very long third arms could belong to a *vulgaris*-like species." The same author (1947) added " whatever they may be they are clearly not the young of any littoral species." Voss (1951) considered the possibility of *M. scorpio* being the larval form of *Scaeurgus* but had insufficient material to reach any decision.

These views reflect the need for clearing up the status of the Atlantic forms of *Macrotritopus*, and except for *M. equivoca* I have been privileged to re-examine all the original material reported on by Degner (1925), Robson (1929), Joubin & Robson (1929) and Voss (1951) together with many additional specimens from the plankton catches of the " Discovery " Investigations, 1925–1939. I have been able to do this through the generosity of Dr. Anton Brunn (for the loan of Dana specimens) ; Dr. Gilbert Voss (for the use of two specimens of *Macrotritopus* from Florida) ; and Dr. N. A. Mackintosh and Dr. Helen Bargmann, for "Discovery" material. I also wish to thank Dr. G. R. de Beer, F.R.S., and Dr. H. W. Parker for valuable suggestions, Mr. G. L. Wilkins for his superb drawings (Pl. 3 and figures 1-6), and Mr. H. O. Ricketts for his great care in examining large samples of plankton for octopod larvae.

(a) *Octopus (Macrotritopus) equivocus* Robson

Octopus gracilis Verrill 1884, p. 236 *non* Eydoux & Souleyet 1852, p. 13.
Macrotritopus equivocus Robson 1929*a*, p. 311.
Octopus (*Macrotritopus*) *equivocus*, Robson, 1929*b*, p. 169.
Octopus (*Macrotritopus*) *equivoca*, Joubin & Robson 1929, p. 93.

TYPE LOCALITY. "Albatross" St. 2084, 40° 16′ 50″ N., 65° 05′ 15″ W., south of Cape Sable, Nova Scotia, 1,290 fms. ; 1 specimen.

TABLE I

Measurements in mm.

Length of body (? ventral mantle length)	11·0
Mantle width	7·0
Interocular width	6·5
Length of head and body	17·0
Arm length :	
1st	19·0
2nd	21·0
3rd	42·0
4th (damaged)	—

Verrill thought that the specimen was a juvenile of a species growing to a large size and was convinced that it was not the young of any known species. He noted the extraordinarily long third arms, the second arms being only half their length. On the evidence available from the description, it agrees with other *Macrotritopus* larvae noted later in having (in alcohol) large purplish chromatophores on the body and the head. There are also purplish spots (i.e., chromatophores) in front of and behind each sucker, this feature being common to all *Macrotritopus* and to many other octopod larvae.

Verrill notes that the first 3–5 suckers on the lower pairs of arms are uniserial and that this arrangement is not found on the dorsal arms. This is unusual, but a minor point, as the arrangement may be due to unequal contraction of the arms during fixation.

Three features about this larva are noteworthy. It is the largest known specimen of *Macrotritopus*; it was caught over deep water and its occurrence (off Nova Scotia) is well to the north of any other records of larvae of this genus.

(b) ***Octopus (Macrotritopus) scorpio*** (Berry)

Polypus scorpio Berry 1920, p. 299, pl. 16, fig. 4.
Octopus (*Macrotritopus*) *scorpio*, Robson 1929*b*, p. 169.
Octopus (*Macrotritopus*) *scorpio*, Joubin & Robson, 1929, p. 93.

LOCALITY. "Bache" St. 10204, off Biscayne Bay, Florida; 20.iii.1914; 75–0 m.; 1 specimen.

Berry gives total length as 22 mm., and 4·5 mm. as dorsal mantle length. The measurements given below have been calculated from his figure in order to provide some basis for comparison with other larvae.[1]

TABLE II

Measurements in mm.

Ventral mantle length	4·73
Dorsal mantle length	5·89
Mantle width	3·85
Interocular width	3·8
Arm length:	
1st	3·1
2nd	7·27
3rd	14·9
4th	4·62
Mantle-arm index	31·8

Berry had some doubts about his species being specifically distinct from Verrill's *gracilis*, but mentioned the inequality in the length of the first and second arms, the still greater length of the third arms and the minute papillations as distinguishing features. The chromatophore pattern is only briefly mentioned.

(c) ***Octopus (Macrotritopus) kempi*** Robson.

Macrotritopus kempi Robson, 1929*a*, p. 311.
Octopus (*Macrotritopus*) *kempi*, Robson, 1929*b*, p. 170.

TYPE LOCALITY. "Discovery" St. 276, 5° 54′ S., 11° 19′ E., off the mouth of the Congo; 5.viii.1927; N 70B, 110–0 metres; 2 syntypes (B.M. 1947.3.12.1–2).

Robson regarded this species as a very distinct one on account of its narrow head, wide mantle, the smooth surface of the skin, the size of the web and the distinctive colour pattern. He also drew attention to the proportions of the third arm, and mentioned that there were 11–12 filaments in each demibranch.

---

[1] Berry's figure is not very satisfactory; the head is said to be "distinctly narrower than the body," but as pointed out by Robson it is nearly as wide as the body in the figure; Berry's "dorsal mantle length" of 4.5 mm. is probably the distance from the apex to the nuchal ridge, and the measurement given in the table is the distance between the apex and the point midway between the eyes.

Robson (1929*b*, p. 171) drew attention to the position where this species was found over deep water and about 10 miles off the edge of the continental shelf. This species is further discussed and the specimens re-described on pp. 76–77.

(d) ***Octopus (Macrotritopus) danae*** Joubin & Robson

Octopus (*Macrotritopus*) *danae*, Joubin & Robson, 1929, p. 87, fig. 1.
Octopus (*Macrotritopus*) *danae*, Joubin 1937, p. 33, fig. 33.

TYPE LOCALITY. "Dana" St. 1152, 30° 17′ N., 20° 44′ W., 23.ix.21 (160 metres). Paratypes from the Western Mediterranean, off Guiana and off W. Cuba.

Joubin and Robson were clearly puzzled about the relationship of their species with previously described forms. However, they created a new species chiefly on the grounds that although the third arms were very long (74–80% of the total length), the second arms were also particularly well developed ; the third arm exceeding the second by 1·7–2·1 times its length. Other differences were mentioned.

The measurements given by Joubin & Robson are given below for seven specimens examined by them.

TABLE III

Measurements in mm.

	No. of specimen.													
	2		1		3		4		5		6		7	
Mantle length (? dorsal)	13		13·5		10		10·5		10		9		12	
Arms :	Left	Right	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.
1st	20	21	16	16	12	14	13	14	13	14	10	—	13	12
	28	32	25	25	22	20	22	21	22	23	17	18	21	19
	48	37	38	36	37	42	37	33	35	35	28	32	39	36
	27	29	20	—	18	18	18	19	17	19	15	12	19	17
Indices :														
Mantle width, percentage length	57		48		60		57		55		61		—	
Head width, percentage length	46		44		50		52		50		55		50	
3rd arms, percentage total length	78		74		80		78		77		78		76	
3rd arm > 2nd arm	1·7 times		1·5		2·1		1·6		1·5		1·7		1·8	

The above figures have not been used in my investigations, and all the specimens which I have been able to see have been measured again as it was desirable to get additional readings.

The "Dana" material forwarded to me, together with paratypes in the British Museum (Natural History), contains a few specimens apparently not seen by Joubin & Robson, so it has been deemed desirable to examine this material in detail in the next section.

(e) ***Scaeurgus*** (Troschel sp. juv.) Degner, 1925

"Thor" St. 184: 38° 10′ N., 22° 23′ E., Gulf of Corinth; 17.viii.1910; 65 metres of wire.

Some octopod larvae from the Mediterranean in which the third arms were particularly well developed and long were described by Degner (1925, p. 79); these are essentially *Macrotritopus*-like forms which have to be considered in any discussion of the *Macrotritopus* problem. Degner assigned these larvae to *Scaeurgus* because one of his specimens was showing the beginning of a hectocotylus on the third left arm. A sinistral hectocotylus is a characteristic of *Scaeurgus* and also of *Pteroctopus tetracirrus*, another Mediterranean species; the latter species was not discussed by Degner in relation to his larvae.

The relationship of these forms to other described species of *Macrotritopus* has not been fully realized by earlier workers, and it is possible that they have been misled by Degner's fig. 52, which portrays a larva quite unlike the usual *Macrotritopus*. It has been possible to re-examine these larvae in this investigation (see p. 74).

C. A RE-EXAMINATION OF *Macrotritopus* LARVAE

All the material of these larvae which it has been possible to gather together has been re-examined. It includes the type material of *Macrotritopus danae*, *M. kempi*, Degner's *Scaeurgus*, two new specimens from Florida (the type locality of *M. scorpio*), as well as some additional specimens brought to light from an examination of hauls made in the tropical Atlantic by the "Discovery" Expeditions (1925–1939).

(a) ***Macrotritopus danae*** Joubin & Robson

Larvae have been available from the following stations of the Danish "Dana" Expeditions 1920–22 (see Schmidt, 1929):

St. 1123^{vii}, 37° 48′ N., 2° 44′ E., Western Mediterranean, 26.ix.21, S. 200, 200 metres of wire; 1 specimen (8·25 mm. in ventral mantle length).

St. 1124^{ii}, 37° 15′ N., 2° 55′ E., Western Mediterranean 27.ix.21, S. 200, 200 metres of wire; 2 specimens (2·5, 6·75 and 9·0 mm. in ventral mantle length); also Joubin & Robson's No. 2 specimen.

St. 1174^{iii}, 5° 35′ N., 51° 08′ W., off Guiana, 16.xi.1921, S. 200, 300 metres of wire; 1 specimen (now dry).

St. 1223^{iv}, 22° 06′ N., 84° 58′ W., off Cuba, 1.ii.22, S. 200, 50 metres of wire; 1 specimen (4·95 mm. in ventral mantle length).

New measurements have been made on the six larvae at my disposal.

No. 1. This specimen, in sea-water formalin, is now rather faded with faint traces of chromatophores only on the third arms. The interbrachial web is moderately developed; its depth in the A sector is about 3·0 mm., and about the same in other sectors (except sector E, where it is distinctly less well developed).

No. 2 is a young and very interesting larva in which the third arm is more than twice the length of the other arms; the latter and the interbrachial web are but little developed. These shorter arms have the thin whip-like tips so characteristic also

Table IV.—*Macrotritopus danae*

Measurements in mm.

	No.					
	1	2	3	4	5	6
Ventral mantle length	8·25	2·5	6·75	9·0	9·75	4·95
Dorsal mantle length	10·8	3·0	11·55	13·35	12·0	5·7
Mantle width	7·05	2·4	6·0	7·35	7·8	3·6
Interocular width	6·45	2·55	4·8	6·75	6·0	4·2
Diameter of eye	2·55	0·9	2·25	2·4	2·55	1·35
Arm length						
1st arm	14·25	1·5	8·7	14·25	15·75	3·0
2nd arm	22·5	1·75	15·45	23·25	27·0	4·95
3rd arm	37·5	4·25	27·75	32·25	33·0	12·75
4th arm	18·0	1·75	11·25	21·0	21·0	4·05
Diameter largest sucker :						
Diam. sucker, 1st arm	0·5–0·55	0·25	0·3	0·5	0·5	0·2
,, ,, 2nd arm	0·55–0·6	0·25	0·4	0·6	0·55	—
,, ,, 3rd arm	0·75–0·8	0·25	0·6	0·75	0·8	0·45
Indices :						
Mantle arm index	22·0	58·8	24·35	27·9	29·6	38·8
Sucker index, 3rd	9·7	10	8·9	8·34	8·21	9·1
,, ,, 2nd	7·28	10	5·93	6·67	5·64	—
,, ,, 1st	6·67	10	4·44	5·56	5·13	4·04

of early stages of *Octopus vulgaris*, and their undeveloped state is reflected in the number of suckers they carry. From the base of the arm there are 3–4 uniserial suckers, 1–2 pairs of biserial suckers followed by rudiments of others. The third arm, however, has about 7–8 well-formed, biserial suckers and rudiments of others towards the tip. All the chromatophores have disappeared.

No. 3. In this specimen the right eye is torn and protruding (allowance has been made for this in measurements) and the third left arm is mutilated. Except for traces of two rows on the outer surface of the third arms the chromatophores have disappeared.

No. 4. The mantle-shape in this specimen is as figured by Joubin & Robson. The interbrachial web is moderately developed, the deepest sector being D. The chromatophore pattern has all but disappeared and there is no trace left on the mantle. On the dorsal head there are two in the position indicated for *M. scorpio* by Berry but the others are very faint. On the third arms there are traces of a few, opposite suckers, and two faintly indicated rows on the outer surface of these arms.

No. 5. This paratype (B.M. 1929.6.29.1.) has retained far more of its colour than any of the other "Dana" larvae ; this is perhaps partly due to the fact that the specimen is in alcohol, and partly also because it has been kept for the greater part of the time in total darkness. However, all chromatophores of the mantle have disappeared except three in a row along the *dorsal* mantle edge and the deep-seated ones of the visceral mass. Those of the dorsal side of the head can be counted and conform to the *vulgaris* pattern.

The chromatophores of the third arms are contracted. On the outer surface there is, proximally, a single row, followed distally by a double row. Here and there there is a suggestion of the pattern seen in *M. kempi*.

No. 6. No trace remains of the original chromatophore pattern.

(b) ***Macrotritopus kempi*** and other "Discovery" larvae

In addition to the syntypes of *M. kempi*, larvae have been found at the following stations of the "Discovery" Expeditions (1925–1939):

St. 276, 5° 54′ S., 11 19′ E., N.W. of mouth of the Congo, 5.viii.1927, TYF, 150(–0) m.; 2 specimens of 3·3 and 4·5 mm. in ventral mantle length.

St. 276, N. 100 B, 110–0 m.; 2 syntypes of *M. kempi* Robson and 1 specimen of 3·75 mm. in ventral mantle length.

St. 290, 3° 25′ 25″ N., 16° 50′ 52″ W., off West Africa. 24.viii.1927, N 100 B, 86–0 m.; sounding 5,165 m.; 1 specimen of 5·4 mm. in ventral mantle length.

St. 1592, 09° 31′ N., 17° 37′ W., off West Africa, 17.x.1935, TYFB, 200–0 m.; 1 specimen of 6·0 mm. ventral mantle length.

St. 1594, 04° 15′ N., 12° 58′ W., off West Africa, 19.x.1935, TYFB, 144–0 m.; 1 specimen of 6·15 mm. in ventral mantle length.

St. 2646, 05° 38′ N., 14° 03′ W., off West Africa, 19.iv.1939, TYFB, 250–0 m.; 1 specimen of 3·2 mm. in ventral mantle length.

St. 2646, TYFB, 1,500–800 m.; 1 specimen of 3·45 mm. in ventral mantle length.

The standard measurements of the Discovery specimens are given in Table V.

TABLE V.

Measurements in mm.

	No.									
	7	8	9	10	11	12	13	14	15	16
Ventral mantle length	8·1	7·65	3·3	4·5	3·75	5·4	6·00	6·15	3·2	3·45
Dorsal mantle length	9·6	9·75	3·75	6·45	4·95	7·05	6·75	9·0	3·9	4·2
Mantle width	9·75	7·8	3·6	3·9	3·75	4·05	4·95	5·85	2·55	—
Interocular width	6·0	5·4	3·3	4·5	3·45	3·75	4·65	5·7	2·70	3·0
Diameter of eye	—	—	—	—	—	—	—	—	1·0	—
Arm length:										
1st	13·5	11·25	2·25	4·2	2·25	5·4	5·25	7·8	1·5	2·40
2nd	22·2	18·0	3·75	6·75	2·70	8·25	8·25	15·0	1·65	3·0
3rd	32·25	—	10·95	16·5	10·5	16·0	15·3	28·5	6·0	6·75
4th	18·45	14·25	2·25	4·5	2·85	6·5	8·25	10·05	1·5	2·25
Diameter, largest suckers:										
2nd arm	0·45	0·35	0·2	0·25	0·2	0·2	0·3	0·4	—	—
3rd arm	0·55	0·5	0·35	0·4	0·35	0·45	0·55	0·55	0·3	0·3
Indices:										
Mantle-arm index	25·15	—	30·15	27·25	33·5	33·75	39·25	21·6	55·0	51·0
Sucker index:										
3rd arm	6·8	6·54	10·6	8·88	9·34	8·33	9·17	8·95	9·1	8·7
2nd arm	5·56	4·58	6·06	5·55	5·33	3·42	5·0	6·5	6·82	—

Nos. 7 and 8 and the holotype and paratype of Robson's *M. kempi*, while Nos. 9, 10 and 11 are also from the same station.

The type is in very good condition, and so is the paratype except that in it both third arms are damaged (the left one was regenerating a new tip). Robson's figure (1929*b*, p. 170, fig. 60) gives a very good impression of the arrangements of chromatophores on the arms and head. On the ventral surface of the mantle, funnel and head the pattern of chromatophores is very like that in *O. vulgaris*. A notable feature in this specimen is the development of the other arms (1, 2 and 4), and the degree of development of the conspicuous chromatophores on them as on the third arm.

On re-examination the head is seen to be rather contracted and the mantle fully inflated in both specimens.

As regards measurements, in the species *M. kempi* the interocular width is very much less than the mantle width—a feature of considerable importance to Robson in defining his species. These specimens were picked out on board and transferred to alcohol with consequent shrinkage of the head region ; this is evident from comparison with other specimens from the same station which were not picked out of the plankton samples (Pl. 3, figs. 1 and 2). After making due allowances for size (and refraining from comment at this point on the relative proportions of the arms) all the specimens from this station undoubtedly form growth stages of one species. The most constant and characteristic feature is the chromatophore pattern of the third arms. On these (and on the second arms only to a lesser degree) the double row of chromatophores on the outer surface is exceptionally clear and distinct, especially the dorsal row. In this row each chromatophore is lengthened at right angles to the axis of the arm, giving the arm the appearance of being banded. On the sides of the third arm there is often a chromatophore at the base of each sucker but sometimes this is placed between the suckers. On the ventral face of the third arm there are also chromatophores between the bases of the suckers.

(c) **Scaeurgus** (Troschel sp. juv.) Degner, 1925

A re-examination of the original larvae lent by the Zoologiske Museum, København, reveals little resemblance between the published figure (Degner, 1925, p. 79, fig. 52) and the eight specimens available for study. In brief, the larvae are very similar in general appearance to other *Macrotritopus* which have been described from the Mediterranean and the Altantic (Text-figs. 1–5). Table VI gives the measurements obtained in 1952.

Degner's specimen No. 2 (specimen H above) is the largest example in this series. It has a ventral mantle length of 6·0 mm. (given as 6·3 mm. by Degner ; the differences between his measurements and mine are probably due to shrinkage in alcohol). Measurements of this and the other specimens from St. 184 are given in Table VI.

It will be seen (Text-fig. 5) that in this late larva and in the younger ones the shape and proportions of the head and mantle are quite unlike Degner's fig. 52, and have the usual form of *Macrotritopus*.

TABLE VI

Measurements in mm.

	A	B	C	D*	E	F	G*	H
Overall length (i.e., including 3rd arm)	10·5	10·95	14·85	10·95	8·55	8·7	9·6	—
Ventral mantle length	3·3	3·9	4·0	3·6	2·7	2·85	3·15	6·0
Dorsal mantle length	4·65	4·85	5·55	4·8	3·9	4·05	3·9	7·05
Mantle width	3·15	2·85	3·9	3·3	2·7	3·0	2·55	4·5
Head width	3·3	2·85	3·3	3·0	2·55	2·4	2·4	3·9
Diameter of eye	1·05	1·3	1·5	1·35	0·85	0·75	1·5	1·65
Arms :								
1st	1·8	2·1	2·55	2·25	2·0	1·25	2·0	4·65
2nd	2·4	2·85	3·15	2·7	2·5	1·75	2·3	6·75
3rd	6·75	5·55	7·95	5·1	3·75	4·0	5·25	15·0
4th	1·8	2·1	3·0	2·55	1·8	1·75	2·0	6·0
Diameter proximal (basal) sucker	0·2	0·2	0·225	—	0·2	0·2	0·18	0·3
Diameter last uniserial sucker	0·25	0·25	0·25	—	0·2	0·2	0·2	0·3
Diameter 1st biserial sucker	0·25	0·25	0·25	—	0·2	0·2	0·2	0·35
Diameter largest sucker (3rd arm)	0·3	0·25	0·3	0·3	0·22	0·22	0·25	0·45

* Specimens D and G are distorted, so that the mantle length for these is estimated.

The chromatophore pattern is rather faded but some features can be distinguished ; those of the dorsal mantle have disappeared, but on the ventral surface there are about 20, scattered over the surface as in *O. vulgaris* larvae of similar size (i.e., in mantle length). Deep-seated chromatophores are present on the dorsal head as in the pattern typical of *O. vulgaris*. On the arms the chromatophores occur in a single row up to the edge of the web and then become double.

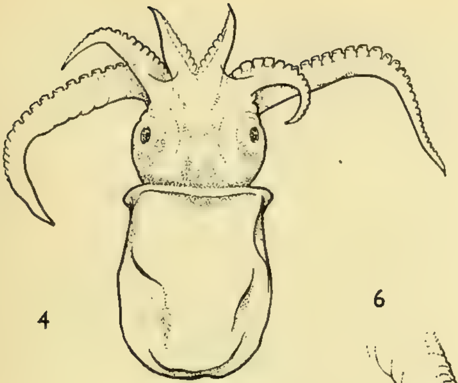
The web is fairly well developed and is of the order D = C > B > A = E. On the first arm it reaches to almost half its length. The body and arms are covered with the remains of *Köllikersche buschel* and some papillae, scattered over the mantle are developing. There are 11 gill filaments in the outer demibranch of the left gill.

The feature of greatest interest is the third left arm, which, according to Degner, was beginning to exhibit hectocotylization. I can make out no details in the structure of the tip of this arm, which is constricted off to form an egg-shaped structure with a slightly-pointed tip ; its size is 0·30 mm. × 0·20 mm. (Text-fig. 6).

The identity of these larvae with *Scaeurgus* or *Pteroctopus* depends on our interpretation of this structure. Is it due to the vagaries of preservation, or can we interpret its symmetrical shape and delicately rounded appearances as a developing hectocotylus ? Consideration of this feature in relation to distribution is deferred to p. 96.

(d) SPECIMENS FROM FLORIDA

Recently G. L. Voss (1951) has mentioned some *Macrotritopus* larvae which he considered to be the *scorpio* form described by Berry (1920, p. 299). By courtesy



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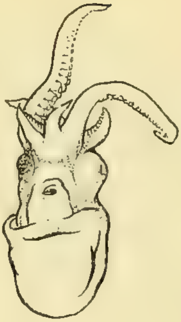

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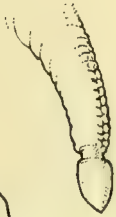

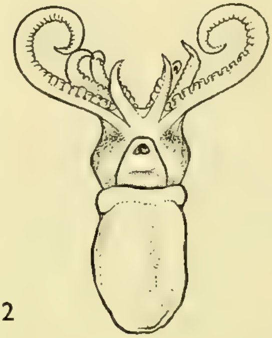

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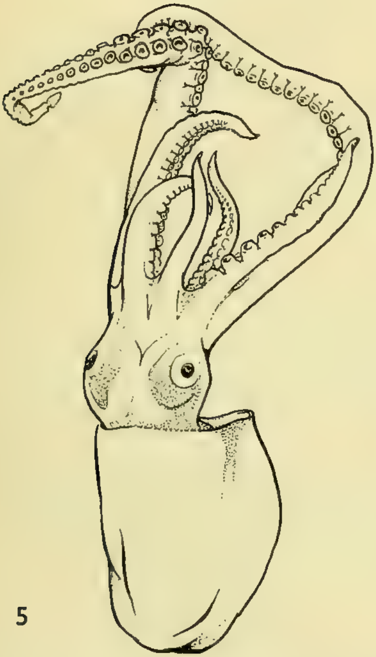

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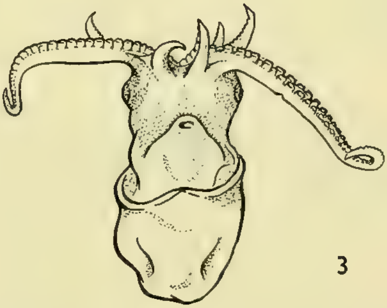

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FIGS. 1–4. *Scaeurgus* sp. Degner, 1925 : the smaller larvae from "Thor" St. 184, Gulf of Corinth ; all approximately × 6.

FIG. 5. *Scaeurgus* sp. Degner 1925: the largest larva from "Thor" St. 184 (specimen H), exhibiting signs of hectocotylization ; × 6.

FIG. 6. *Scaeurgus* sp. Degner : tip of the third left arm from specimen H with rudimentary hectocotylus ; greatly enlarged.

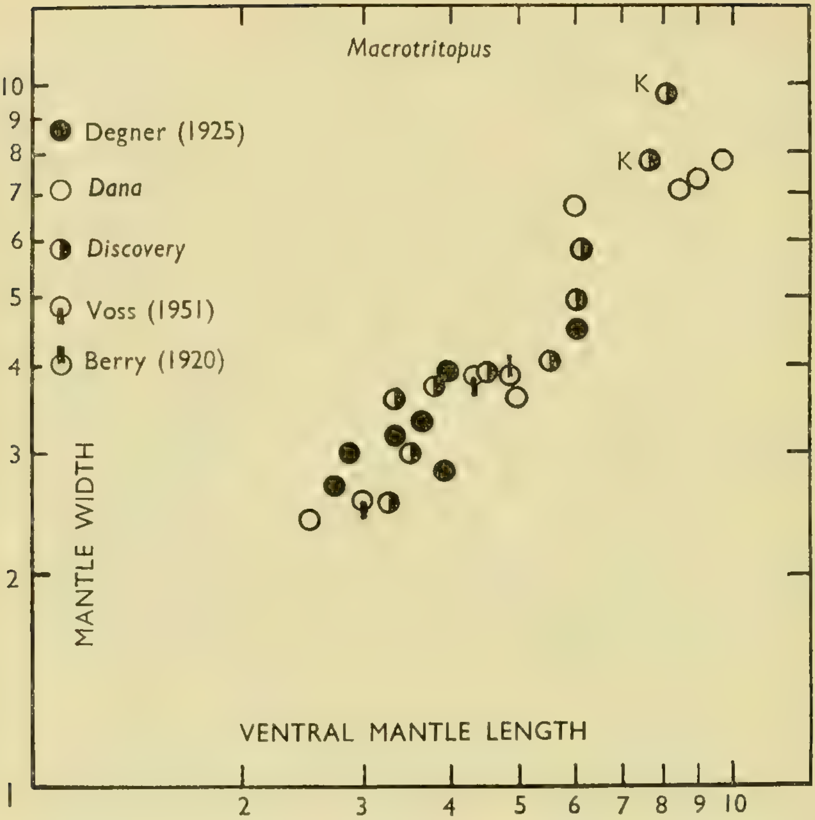

FIG. 7. Relationship between mantle width and ventral mantle length in *Macrotritopus danae*, *M. kempi*, *M. scorpio*, *Scaeurgus* sp. Degner and in additional specimens from the "Discovery" Expeditions (1925–1929). The letter *k* denotes the type material of *M. kempi*. All measurements in figs. 7–17 are in millimetres.

of Mr. Voss I have been able to examine two of the larval forms he mentions ; one is in formalin and the other (No. 18) in alcohol.

I was unable to see much pattern on the surface of these larvae as their pigment has largely disappeared, presumably through exposure to sunlight after fixation. However, such pattern as remained indicated that there was nothing unusual about it, and that it was probably no different in this respect from other *Macrotritopus* larvae I had seen.

TABLE VII.—Macrotritopus *larvae from Florida*

Measurements in mm.

	No.	
	17	18
Ventral mantle length	4·35	3·0
Dorsal mantle length	4·8	3·3
Mantle width	3·9	2·55
Interocular width	3·75	2·5
Arms :		
1st	3·15	1·3
2nd	4·95	1·5
3rd	10·2	6·0
4th	3·0	1·5
Diameter, basal sucker	0·2	0·125
,, second uniserial sucker	0·25	0·15
,, first biserial sucker	0·25	0·2
,, largest sucker, 3rd arm	1·2	0·3

D. A COMPARISON OF THE SPECIES

It was recognized quite early in the investigation that some or all of the Mediterranean-Atlantic species of *Macrotritopus* might prove to belong to one or two species, and the problem was to distinguish between growth stages and specific differences. Accordingly some characters which might reveal significant points of difference were examined.

Here it may be convenient to mention that *ventral* mantle length is used throughout in all calculations involving mantle length. It appears more reliable than the usually accepted dorsal mantle length (mid-point between the eyes to the apex of the mantle), because retraction of the head in the larva can make as big differences in measurements as distortion of the mantle margin. In the larva, too, there is a distinct ridge on the dorsal mantle which provides a useful check if by chance the ventral mantle edge is distorted.

All the accompanying graphs (except Text-figs. 9 and 10) are plotted on Wrightman's double logarithmic paper to demonstrate the relationships of the various parts. In using the data from this assorted collection of octopus larvae I have been very conscious of the inadequacy of the material, and for this reason statistical methods have not been exploited. It is, however, surprising in view of the assortment of material how well grouped the measurements are in relation to straight lines.

It became obvious early in the investigation that material in alcohol, notably Degner's *Scaeurgus* and Robson's two syntypes of *Macrotritopus kempi*, were much shrunk, the shrinkage affecting different parts unequally. With age, too, shrinkage progresses, and it must be remembered that the "Thor" collections were made 40–50 years ago and those of the " Discovery " between 1925 and 1939. Similarly the material of *M. danae* and larvae from the " Discovery " collections, although both are in formalin, are not strictly comparable from a preservation point of view, the former being flaccid (and possibly a little swollen ?) by comparison with the latter,

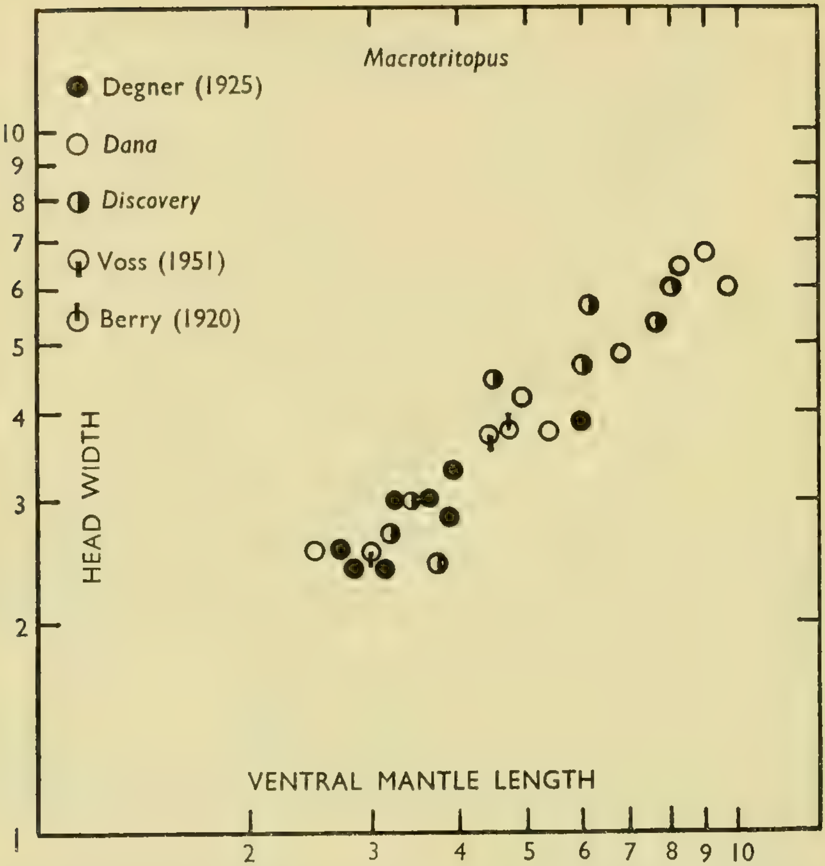

FIG. 8. Relationship between head width and ventral mantle length in *Macrotritopus danae*, *M. kempi M. scorpio*, *Scaeurgus* sp. Degner and in additional specimens from the "Discovery" Expeditions (1925–1929).

which are in fine condition. Widely different results can be obtained even with the same medium from slight differences in the method of fixation, particularly in soft-bodied animals without any substantial skeletal structures. The octopus arms in particular are highly contractile, and it is by no means improbable that in their extended condition they were two and even three times the length recorded after preservation.

(a) MANTLE LENGTH. At sizes below 4 mm. in ventral mantle length there is very little difference between the length and the width of the sac.[1] Above this size the mantle becomes distinctly elongated, except in the syntypes of *M. kempi*, where it is decidedly inflated, giving an erroneous impression of mantle proportions (Text-fig. 7, *k*). On the basis that all the specimens are growth stages, there are no significant differences in the mantle proportions of the different species, although the rather irregular plotting indicates that mantle width is not a useful diagnostic character. This is to be expected, because the mantle sac is a highly muscular pumping organ subject to alternate contraction and expansion.

---

[1] Mantle width, head width and sucker diameter grow in direct proportion to the length of the mantle Text-figs. 7, 8 and 15).

(b) HEAD WIDTH. There are no features about head-width to suggest any significant differences between the species (Text-fig. 8).

(c) THE ARMS. The extraordinary length of the third arm in relation to arms 1 and 2 is very striking in all the small and medium-sized larvae (Plate 3, figs. 3 and 4), but in the large ones the second arm may be 80% of the length of the third arm. Earlier workers, notably Berry (1920) and Joubin & Robson (1929), were greatly concerned with the relative proportions of these three pairs of arms, and although they had some suspicions that discrepancies in relative arm lengths might be accounted for by growth, nevertheless created species largely on these differences.

No one would deny that Degner's larvae belong to one species, although they range from 2·7–6·0 mm. in ventral mantle length. By plotting the measurements of the arms in relation to ventral mantle length in a simple graph we get the results shown in Text-fig. 9; this clearly indicates that differences in arm lengths may be accounted for by growth. A similar impression is gained from plotting the measurements for "Dana" and "Discovery" specimens in the same way (Text-fig. 10).

In the youngest known stages (2·5–3·0 mm. in ventral mantle length) the arms are already differentiated in length with the third arms greatly exceeding the second pair, which in turn are a little longer than the first pair. Between 3·0 and 4·0 mm. the difference in length between the first and second arms becomes more marked, and beyond this all three arms (1, 2 and 3) are growing rapidly.

These simple graphs suggest that the changes in relative proportions of the arms may indicate stages in allometric growth. In Text-figs. 11–13 the arm-lengths (arms 1, 2 and 3) are plotted according to the species or source of the material and for each we get a reasonable plotting, which again suggests that they all belong to one species, and it can be said that in all three arms growth is proportional to the mantle growth.

When the results for the three pairs of arms are grouped, the resulting graph demonstrates that all three grow at approximately the same rate (Text-fig. 14). The rate of growth is indicated by the slope of the mean, and it will be seen that the growth rate is the same in arms 1 and 3, but arm 2 may be growing at a slightly faster rate than the other two. The differences in arm length are dependent on when growth begins; in arm 3 it begins at a ventral mantle length of about 1·4 mm., that is, at hatching size if we assume that the larva comes from a typical octopus egg. The second arm does not begin to grow until the larva has a ventral mantle length of about 2·3 mm.; it is closely followed by the first arm when the ventral mantle length reaches 2·5 mm.

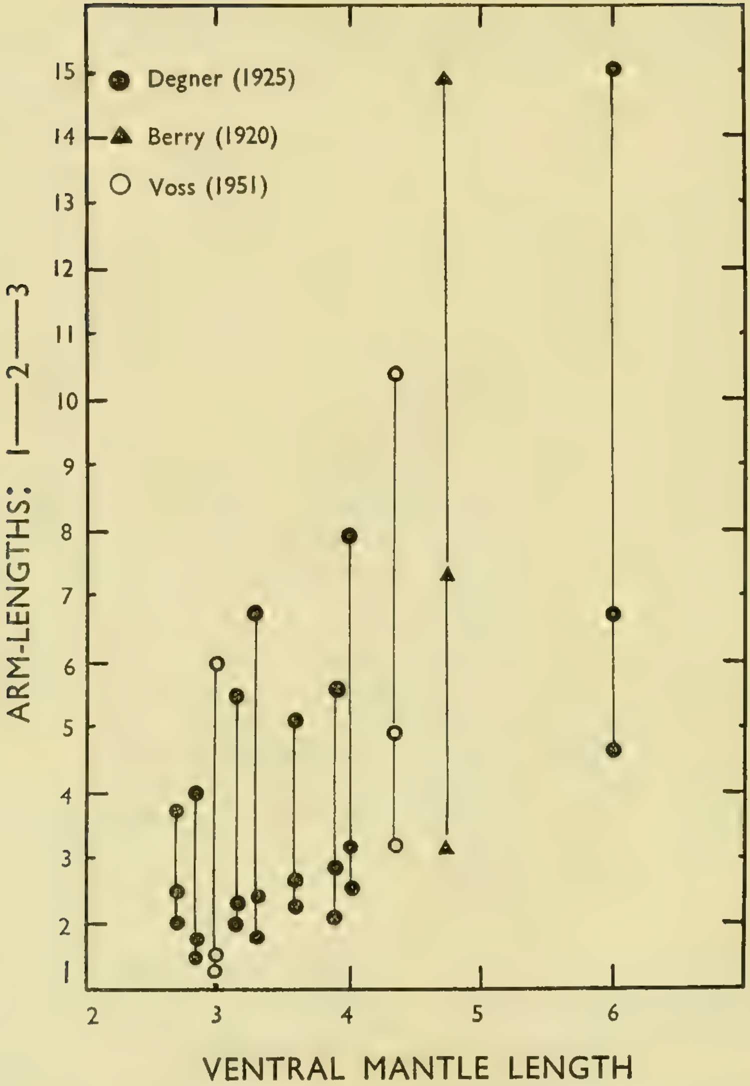

FIG. 9. Length of arms 1, 2 and 3 in relation to ventral mantle length in *Scaeurgus* sp. Degner (filled circles) and *Macrotritopus scorpio* Berry (open circles and triangles), plotted on ordinary graph paper.

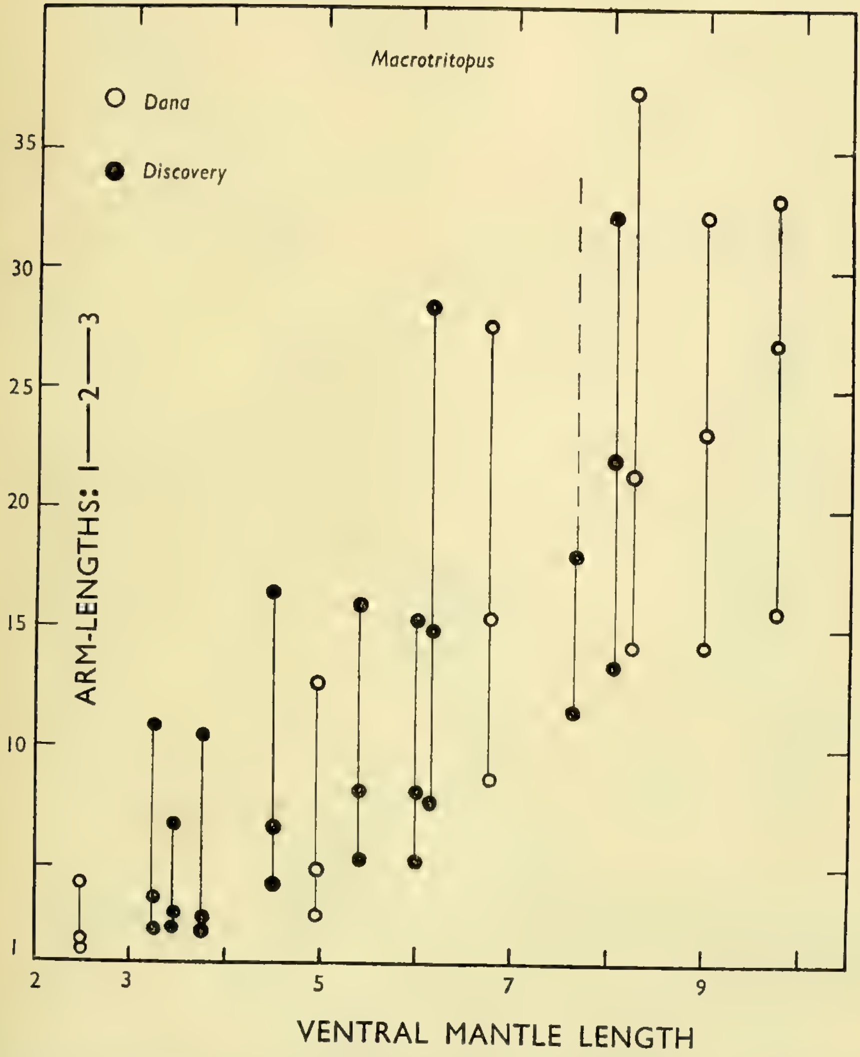

Fig. 10. Length of arms 1, 2 and 3 in relation to ventral mantle length in material from the Danish " Dana " Expeditions 1921–1922 (open circles) and from the " Discovery " Expeditions, 1925–1939 (filled circles), plotted on ordinary graph paper.

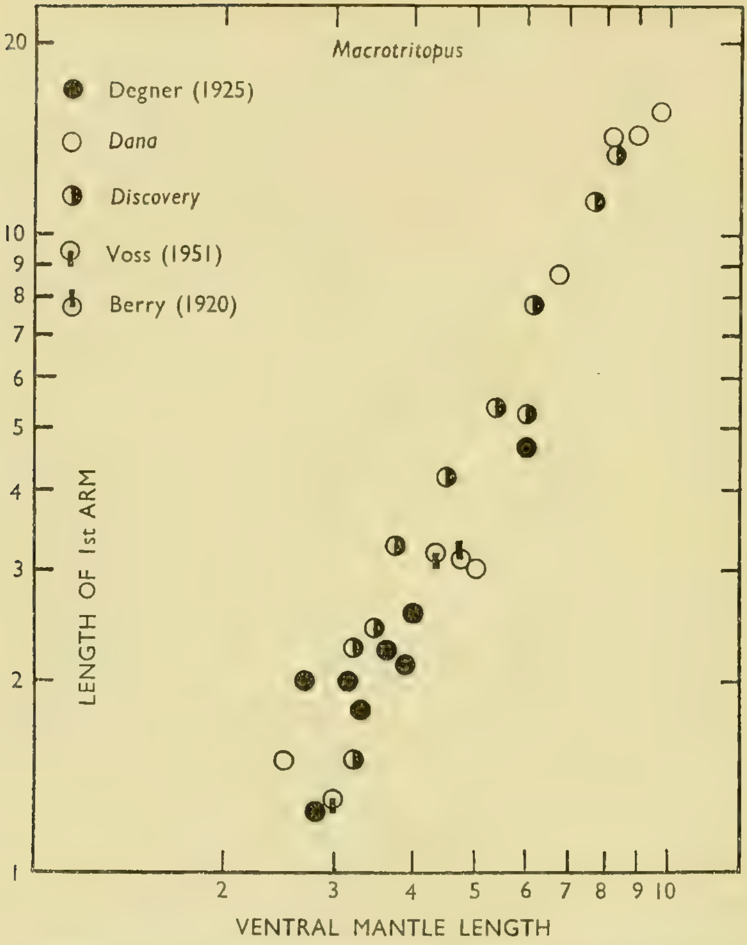

FIG. 11. Relationship of the length of the first pair of arms to ventral mantle length in *Macrotritopus danae, M. kempi, M. scorpio, Scaeurgus* sp. Degner, and in additional specimens from the " Discovery " Expeditions (1925–1939).

(d) SUCKER DIAMETER. The diameter of suckers of the third arm have been plotted in relation to ventral mantle length (Text-fig. 15) ; this graph shows more clearly than the others the shrinkage caused by storage in alcohol compared with formalin preservation. Most of the *Scaeurgus* larvae and the syntypes of *Macrotritopus kempi* (marked *k*) fall well below the line. Apart from this the graph reveals no significant differences between the species.

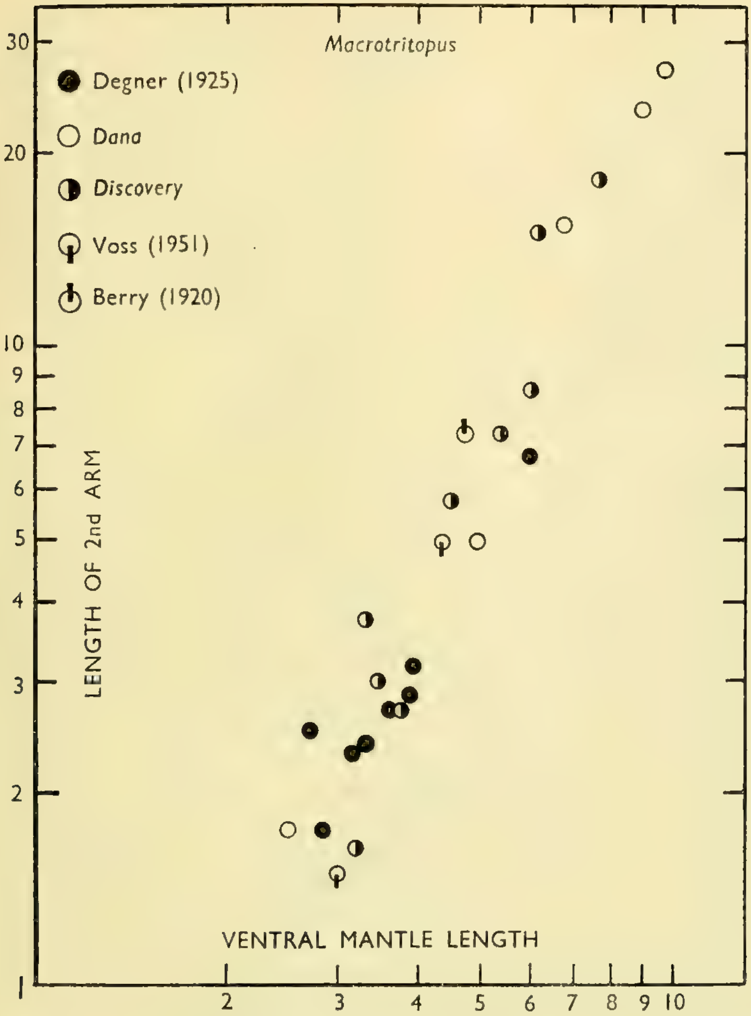

FIG. 12. Relationship of the second pair of arms to ventral mantle length in *Macrotritopus danae*, *M. kempi*, *M. scorpio*, *Scaeurgus* sp. Degner, and in additional material obtained by the " Discovery " Expeditions (1925–1939).

(e) THE RADULA. The radula of a specimen from " Discovery " St. 1592 has been examined. It exhibits a symmetrical $^{A}3$–4 seriation of the cusps of the rhachidian, but there is some irregularity (perhaps to be expected in a young specimen). The first lateral tooth is narrow with a short pointed cusp, and the second lateral has a

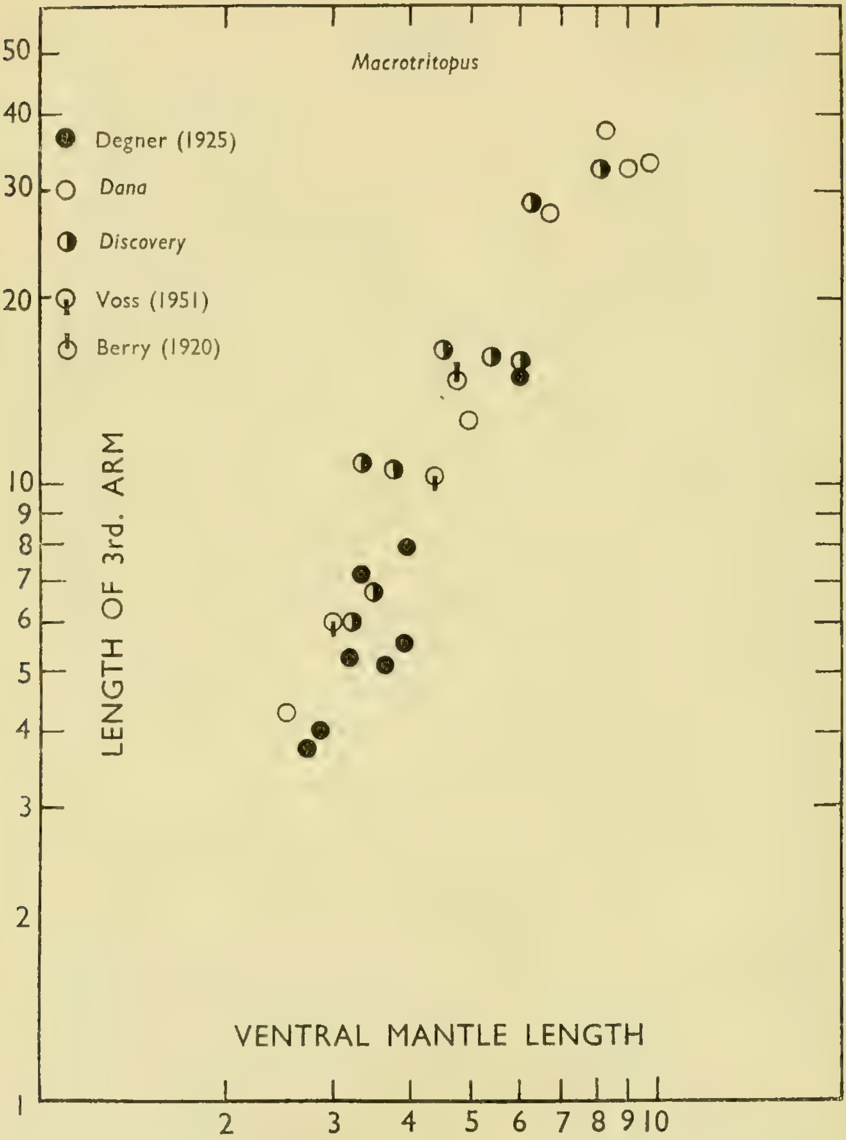

FIG. 13. Relationship of the third pair of arms to ventral mantle length in *Macrotritopus danae, M. kempi, M. scorpio, Scaeurgus* sp. Degner, and in additional material obtained by the " Discovery " Expeditions (1925–1939).

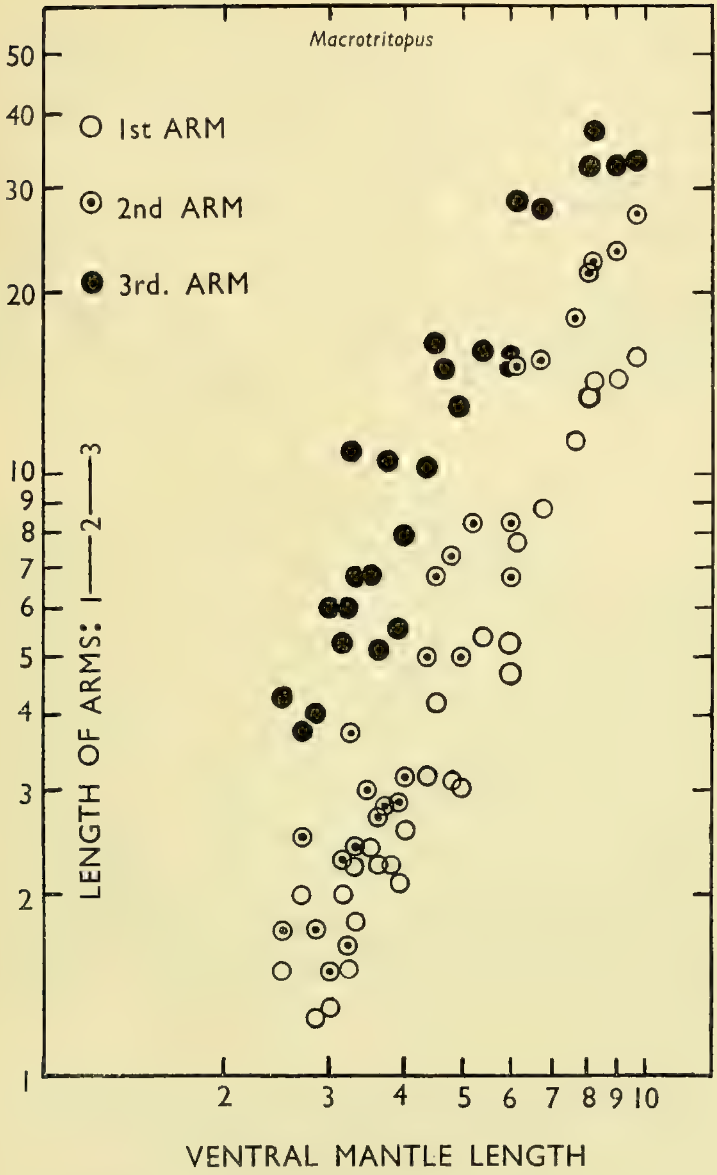

FIG. 14. Relationship of arms 1, 2 and 3 in relation to ventral mantle length in all the specimens examined.

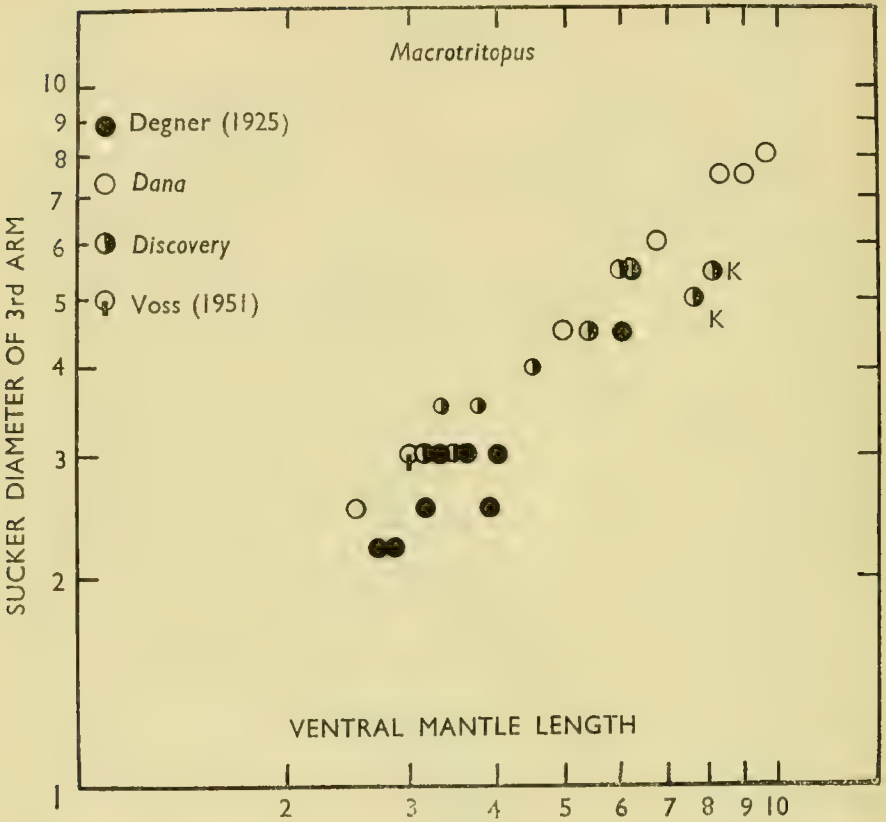

FIG. 15. Relationship of the sucker diameter of the third arm to ventral mantle length in *Macrotritopus danae, M. kempi, M. scorpio, Scaeurgus* sp. Degner, and in additional material obtained by the "Discovery" Expeditions (1925–1939). The letter *k* denotes the type material of *M. kempi*.

well formed endocone but no ectocone. The third lateral is distinctly long, slender and rather curved. The marginal plates are lozenge-shaped, a little broader than long.

The radula of the holotype of *Macrotritopus kempi* has also been examined and is very similar to the above, although details of the seriation of the cusps are difficult to interpret. Even though the preparation is a poor one, the cusps have a symmetrical arrangement and not an asymmetrical one as stated by Robson (1929, p. 312). The laterals are very similar to those of the specimen from " Discovery " St. 1592.

(f) GILL FILAMENTS. The number of gill filaments per demibranch has been noted in one specimen of each of the following : *Scaeurgus* sp. Degner, E. Mediterranean, 11 filaments ; *Macrotritopus kempi* Robson, West Africa, 11–12 filaments ; *Macrotritopus danae* Joubin & Robson, W. Mediterranean, at least 11 ; *Macrotritopus danae* Joubin & Robson, off Cuba, at least 11.

The third and fourth specimens listed above have deteriorated considerably in formalin, and the detailed structure of the gills, is not now very satisfactory for counting filaments.

All the evidence suggests that all the *Macrotritopus* larvae examined belong to a single wide-ranging species. I have not seen Verrill's *Macrotritopus* (*M. equivocus* Robson), but there appears to be no doubt about its identity with the other larvae ; it appears to be nothing more than a very large larva carried by water movements well beyond its normal range.

E. THE BREEDING SEASON

On the assumption that all the larvae belong to a single species it is possible to get some indication of the breeding period. We have to assume that once the eggs are laid (presumably at moderate depth) they take at least as long, if not longer, to hatch as in a littoral octopod. In *Octopus vulgaris* this is a period of 21–30 days, according to temperature, and it may be even longer in a deep-water species where sea temperature on its spawning grounds is likely to be lower.

In order to supplement the data obtained from the material studied, I have drawn on a list of occurrences given by Joubin (1937, p. 36) in addition to my own material. In the latter (Text fig. 16) ventral mantle length is taken as a criterion of size, while in the former overall length appears to be quoted (Text-fig. 17). As breeding may be largely controlled by temperature, the Mediterranean records have to be treated separately from those of the tropical Atlantic.

(a) THE MEDITERRANEAN. In this warm temperate area we have records of larvae of all sizes but only for the months of August and September. It is true that during the Third " Dana " Expedition in 1921–22 the Mediterranean was visited only between 21st September and 4th October, 1921. The earlier expedition in the " Thor " (1908–1910) did, however, cover a much longer interval of time (14th December, 1908, to 21st February, 1909, and 26th June, 1910, to 7th September, 1910) but recorded larvae only in August.

If, as the meagre evidence suggests, larvae are common only in August and September, spawning must take place in June–July and possibly in August as well. By the end of September, when the largest larvae have been found, the majority are ready for settlement on the bottom, while a few late larvae may persist well into October. This is in agreement with Naef's statement that octopod larvae at Naples

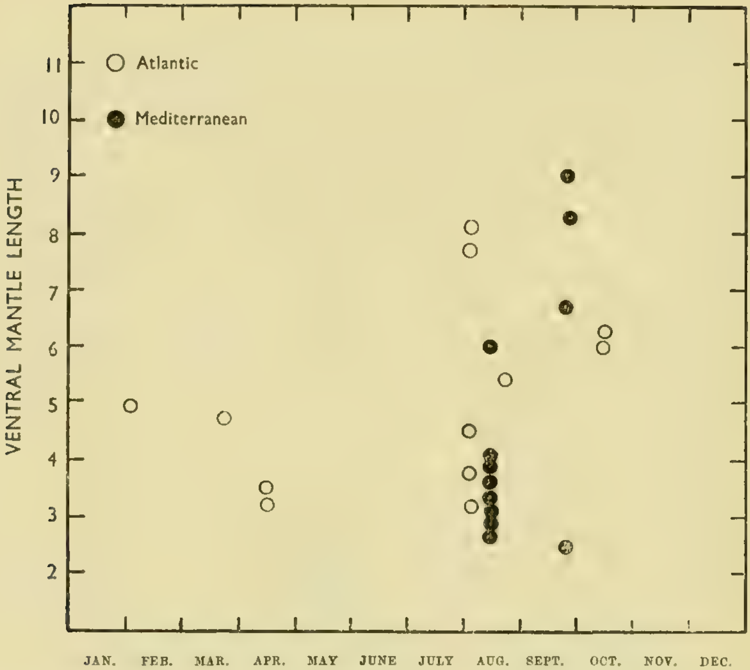

FIG. 16. Size (ventral mantle length) in relation to seasonal occurrence in the Atlantic and Mediterranean.

are more common in August and September than during other times of the year and suggests summer breeding.

(b) THE ATLANTIC. In the Atlantic only two larvae have been found to the north of 30° N. They were found at the following positions:

"Dana" St. 1152, 30° 17′ N., 20° 44′ W., S.W. of Madeira, 23.x.1921; 1 specimen of 18 mm.

"Dana" St. 1341, 33° 15′ N., 68° 20′ W., between Bermuda and the mainland, 14.v.1922; 1 specimen of 20 mm.

All the remainder were found in tropical or sub-tropical waters off West Africa and on the American coast, mainly off islands of the Greater and Lesser Antilles.

On the African coast the ships of the "Discovery" Committee took specimens in March, April, August and October during transit voyages to and from the Antarctic. There has, however, been no continuous sampling on this coast to give an accurate picture of seasonal distribution.

In the Central American region however the "Dana" was constantly taking plankton hauls between November, 1921, and May, 1922. There was no month in this period when larvae were not present. This implies that the breeding period was spread over the whole of this time, and if we take the records from West Africa and Florida into consideration, June is the only month for which larvae have not been recorded, and this apparent absence seems to be due to lack of observations.

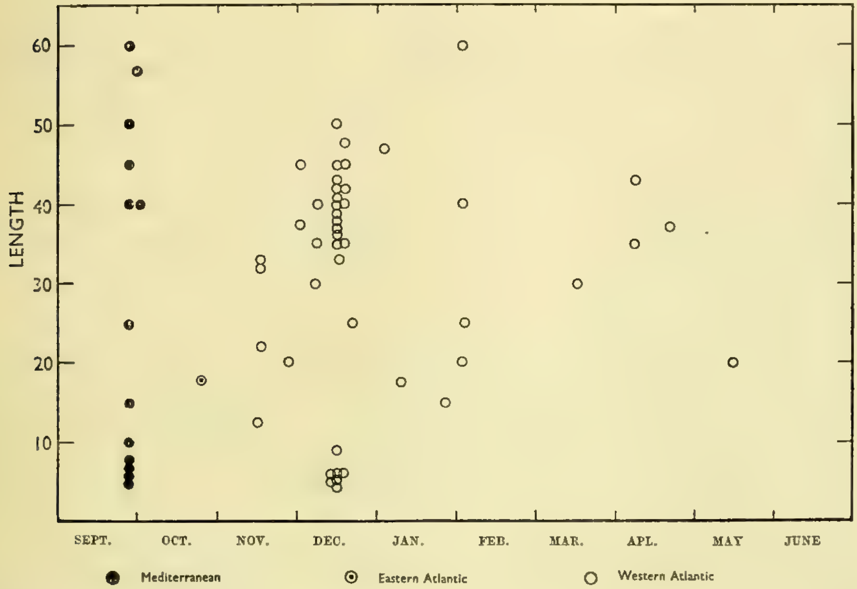

FIG. 17. Size (overall length) in relation to seasonal occurrence in the Atlantic and Mediterranean based on records of *Macrotritopus* spp. from the cruises of the "Dana" (1921–1922).

It is therefore clear that breeding may be noted in tropical and sub-tropical waters throughout the year. The greatest number of larvae (31) was taken in December, but the significance of this is not known. It may be that plankton hauls during this month were made in an area where there was concentration of breeding adults, or it might mean that this was the period of maximum breeding activity. If the latter it would imply maximum breeding in winter in the tropics—contrasting with summer breeding in the more temperate Mediterranean. In the Tropics, however, the factors which may exercise a big influence on temperature (which governs breeding) are local hydrographic conditions. For an animal which lives on the narrow coastal shelf (as off West Africa and the Antilles) local temperature conditions are bound to vary enormously according to movements of water masses, especially upwelling. Local breeding may therefore vary according to place and season.

F. THE SIGNIFICANCE OF THE *Macrotritopus* LARVA

The plankton life of the larvae of *Octopus vulgaris* (to judge from results hitherto unpublished) may have a duration of at least four weeks, and possibly eight or ten weeks under normal hydrographic conditions. For *Macrotritopus* it is reasonable to suppose a planktonic life of longer duration (perhaps for three to five months) on the basis that the larvae reach a much larger size. There is, however, another factor to be considered ; one of Degner's larvae from the comparatively shallow Gulf of Corinth was developing a hectocotylus at 6·0 mm. in ventral mantle length. To judge from evidence from all sources, including Naef's work in the Mediterranean, metamorphosis (here interpreted as the abandonment of a planktonic or pelagic phase) also means the beginning of sex differentiation and the development of gonads ; in the male the visible outward sign is the development of a hectocotylus. In the Gulf of Corinth the water is not very deep, and a larva ready to become benthic should find a suitable bottom at the right time, so that there would be no great delay in settlement. This implies that the ordinary *Macrotritopus* larva completes its planktonic phase at 6–7 mm. in ventral mantle length (allowance being made for the shrinkage of this material).

Other *Macrotritopus* larvae, however, reach a much bigger size without developing any sign of hectocotylus or of gonads. In *M. equivocus* the ventral mantle length is estimated to be 11 mm. ; in *M. kempi* and *M. danae* respectively it is 8·1 mm. and 9·75 mm. In view of the fact that I can find no other differences between these larvae and Degner's species, some other explanation must be sought for the non-appearance of signs of sexual differentiation or maturation, and I am inclined to interpret these large larvae as extended pelagic phases.

This phenomenon has been noticed before in marine invertebrates, but its significance does not seem to have been discussed in relation to distribution and dispersal. It is known from the work of Dr. Marie V. Lebour that in many molluscs a creeping-swimming stage of several days' duration is reached during metamorphosis, which, as suggested by Wilson (1937), may enable the larva to persist in a state whereby it can be swept away by currents to a more suitable substratum. From our present knowledge of the change to a benthic stage it is evident that species with a quick metamorphosis can delay settlement for several days, thus giving them a better chance of finding a suitable bottom.

When metamorphosis is gradual, settlement can be delayed for a long period, as has been demonstrated by Day & Wilson (1934) for the polychaete *Scolecolepsis fulginosa*. During this period of uncertainty the worm continues to grow beyond the 14-setiger stage at which these authors found metamorphosis to take place. In another polychaete, *Loimia medusa*, Wilson (1928) found that its planktonic existence ended when the larva had reached a length of about 6·0 mm. At this size the first pair of gills is beginning to divide, the second is only a rudiment and the third has not made its appearance. Still larger larvae were referred to the species by Monro (1930 and 1931) ; of these the largest example from " Discovery " St. 102 was 15 mm. long and had three pairs of well-developed gills. If we accept the view (as is most likely) that these larvae belong to the widely-distributed *Loimia medusa*, they can only be interpreted as an extended pelagic phase.*

Gurney (1942, pp. 71–75) gives details of several larvae of decapod crustacea which have been caught at sizes well above the known size for moulting into post-larvae. He was " reluctant to accept any theory of abnormality " for these giant larvae, and supposes that they had failed to metamorphose at the right time and continued to grow." He adds : " . . . in a situation like that of Bermuda, where abyssal depths are so close to the shore, it must be quite usual for larvae to find themselves over deep water at the time of metamorphosis."

Similarly when the distribution of *Macrotritopus* larvae is considered many of them were also taken fairly close to land, but in deep water off the edge of the continental shelf. At the places where they were taken (off West Africa and in the Antilles) the continental shelf is very narrow, so that the chances of larvae being swept over deep water are great. On the West coast of Africa, particularly, this seems to occur, and Knudsen (1950) attributes the high percentage of gastropods with very short planktonic or non-pelagic development on this coast to the influence of water movements in eliminating species with planktonic stages of long duration.

The *Macrotritopus* larva with its long third arms (which may be as useful as the squid's tentacles in catching food), its narrow squid-like profile and its curious colour pattern recalling that of the epipelagic larvae of the Cranchiidae, seems well adapted for a pelagic life. It may be that *Macrotritopus* specimens of above 6–7 mm. in ventral mantle length are larvae which have grown large in the plankton because they have not been able to find a suitable bottom (or a suitable bottom at the right depth) for metamorphosis. In other words delayed settlement has resulted in an extended pelagic phase which may be of considerable significance in dispersal. What is important is that it can travel immense distances in the plankton. The *M. equivocus* found off Cape Sable, Nova Scotia, had reached a mantle-sac length of 11 mm., and must have been transported for hundreds of miles by currents (probably from the Carribean or Florida) ; it was likely to be well out of the area in which it could survive as an adult. It may, however, be pertinent to draw attention to the rôle of the extended pelagic phase in maintaining uniformity in a wide-ranging species.

The remarkable similarity of populations of *Scaeurgus* from the Atlantic and Pacific was noted by Berry (1914, p. 306), who adds (*in litt.*, quoted by Voss, 1951) : " if it really is all one species, then there must be some special reason for lack of divergent speciation, and I can conceive no sensible explanation for this in a bottom form except for the possession of a planktonic larval stage of some duration."

G. THE IDENTITY OF *Macrotritopus* WITH *Scaeurgus*

When it became obvious that all the Altlantic *Macrotritopus* were referable to a single species, it was deemed possible to suggest a possible adult with which they could be linked. When this paper was in early stages of preparation in 1950 there were four species with one of which they could possibly be linked, namely, *Octopus vulgaris*, *O. macropus*, *Scaeurgus unicirrhus* and *Pteroctopus tetracirrhus*.

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* Dr. Gunnar Thorson has kindly drawn my attention to Lemche's observations on the North Atlantic tectibranch *Diaphana minuta* Brown, which seem to suggest that the larva of this mollusc is able to delay metamorphosis when swept our over deep water (Thorson, 1946, p. 466 and Lemche, 1948, p. 9). In shallow water adults the embryonic shells are much smaller than those in specimens from depths exceeding 1,000 m. These larger embryonic shells are believed to indicate delayed settlement and resulting growth of the larval shell in specimens which have metamorphosed in deep water.

The first, *O. vulgaris*, was the only species which had a known distribution corresponding most closely to that of the larvae (*Macrotritopus equivocus* being considered to have been carried well out of its normal distribution area). The details of the structure of the radula—asymmetrical in *O. vulgarus* and symmetrical in *Macrotritopus*—together with the occurrence of a normal larva of *vulgaris* in the same hauls as *M. kempi* (St. 276) were sufficient evidence that *O. vulgaris* could not be the adult.

The second, *O. macropus* Risso, has a similar but a more restricted distribution in the Mediterranean and both sides of the tropical Atlantic. This species, too, was ruled out because the details of the radula showed specific differences, and also because larvae of *O. macropus* were positively identified during the investigations.

Scaeurgus unicirrhus and *Pteroctopus tetracirrhus* were originally included in the list of possible adults, not because of any great similarity between the known distribution of the adults and that of *Macrotritopus*, but solely because each species had a sinistral hectocotylus. Degner's largest larva (specimen H) had a swelling at the tip of the third left arm, and on re-examination of the species I found it difficult to imagine its delicately rounded structure being the result of any malformation of the tip of the tentacle, and had to conclude that it was a true rudiment of a hectocotylus.

Evidence from distribution of the adults was not encouraging in 1950, especially as neither species had been found on the American side of the Atlantic and records outside the Mediterranean were very few. However, Voss (1951) gave the first records of *Scaeurgus* from the Western Atlantic (Florida), and Adam (1952) recorded *Pteroctopus* from West Africa. Full records of the two species outside the Mediterranean (where both are found) are given below :

> *Scaeurgus unicirrhus* : Pacific Ocean ; Hawaiian Islands (Berry, 1913 and 1914 as *patagiatus*) ; South of Kyushu (Sasaki, 1920 and 1929 as *patagiatus*) ; Indian Ocean ; Saya de Malha (Robson, 1921) ; Atlantic Ocean, Florida (Voss, 1951).
>
> *Pteroctopus tetracirrhus* : Atlantic Ocean ; Cape Verde Islands (Fischer & Joubin, 1906 and 1907) ; Azores (Joubin, 1900) ; off the coast of Africa (Adam, 1952).

Scaeurgus appears from our present knowledge of distribution to have a much wider range than *Pteroctopus* ; as both species live on moderately deep bottoms, it it not surprising that there are so few tropical records in view of the difficulties of operating trawls in areas where the bottom is covered with living or dead coral.

Both these species have a symmetrical arrangement of cusps on the rhachidian tooth of the radula as in *Macrotritopus*. A closer examination of the *Macrotritopus* radula shows that it agrees well with *Scaeurgus*, and differs from *Pteroctopus* in having a narrower first lateral tooth, a longer, more slender and more curved third lateral, and lozenge-shaped marginal plates. In *Pteroctopus* (see Adam, 1952, fig. 55) the marginal plates are wider and slightly curved in outline.

All the evidence suggests that *Macrotritopus* is the larval stage of *Scaeurgus unicirrhus*, and at present there is no indication that more than one species is involved. *Scaeurgus* has been found in the warm waters of all oceans, and its wide distribution (surprising in a bottom-dwelling animal) has clearly been achieved by this striking pelagic larva. The number of gill filaments per demibranch in *Scaeurgus* (11–14) is exceptionally high for a benthic octopod living at considerable depths near the edge of the continental shelf, but is probably related to the pelagic requirements of the larva.

H. CONCLUSION

All four Atlantic species of *Macrotritopus* have been demonstrated to belong to one species, also now linked with its adult, *Scaeurgus unicirrhus* (Delle Chiaje). *Macrotritopus* falls into the synonymy of *Scaeurgus*, and the position regarding the species is summarized as follows:

Scaeurgus unicirrhus (Delle Chiaje).
  Octopus gracilis Verrill, 1884, p. 236 *non* Eydoux & Souleyet, 1852, p. 13.
  Macrotritopus gracilis, Grimpe, 1922.
  Macrotritopus equivocus Robson, 1929*a*, p. 311.
  Octopus (*Macrotritopus*) *equivocus*, Robson, 1929*b*, p. 169.
  Octopus (*Macrotritopus*) *equivoca*, Joubin & Robson, 1929, p. 93; Joubin, 1937, p. 34.
  Polypus scorpio Berry, 1920, p. 299.
  Octopus (*Macrotritopus*) *scorpio*, Robson, 1929*b*, p. 169; Joubin & Robson, 1929, p. 93.
  Macrotritopus kempi Robson, 1929*a*, p. 311.
  Octopus (*Macrotritopus*) *kempi*, Robson, 1929*b*, p. 170.
  Octopus (*Macrotritopus*) *danae* Joubin & Robson, 1929, p. 87; Joubin, 1937, p. 33.
  Macrotritopus spp. Joubin, 1937, p. 36.
  Scaeurgus (Troschel sp. juv.) Degner, 1925, p. 79.

The great length of the third arm is a larval character only, for it is not found in the adult, in which the arms are subequal. The long third arm may have some special significance in larval life, serving perhaps for capturing food in the same way as the tentacles of the epipelagic squids. The high number of gill filaments, too, indicates an active larval existence which is in contrast with the low number found in octopods like *Bathypolypus* and *Bentheledone*, which are benthic deep-water octopods of the continental slope.

The records indicate that the *Macrotritopus* larva lives in the upper 200 metres. Most of the hauls from deeper water were made with open nets, so that positive conclusions cannot be reached from them, but the specimen taken by the "Discovery" with a closing net between 1,500 and 800 metres was at a surprising depth in a species which has all the appearance of being a surface form. Its occurrence at this depth suggests that it was seeking bottom preparatory to metamorphosis.

If we accept the occurrences of *Macrotritopus* larvae in the vicinity of land (or near the edge of the continental slope) as evidence of the existence of benthic adults nearby, *Scaeurgus* has a more general distribution in the warmer waters of the Atlantic than hitherto supposed. As already mentioned, the difficulties of trawling over coral in the tropics probably accounts for the scarcity of records of the adult.

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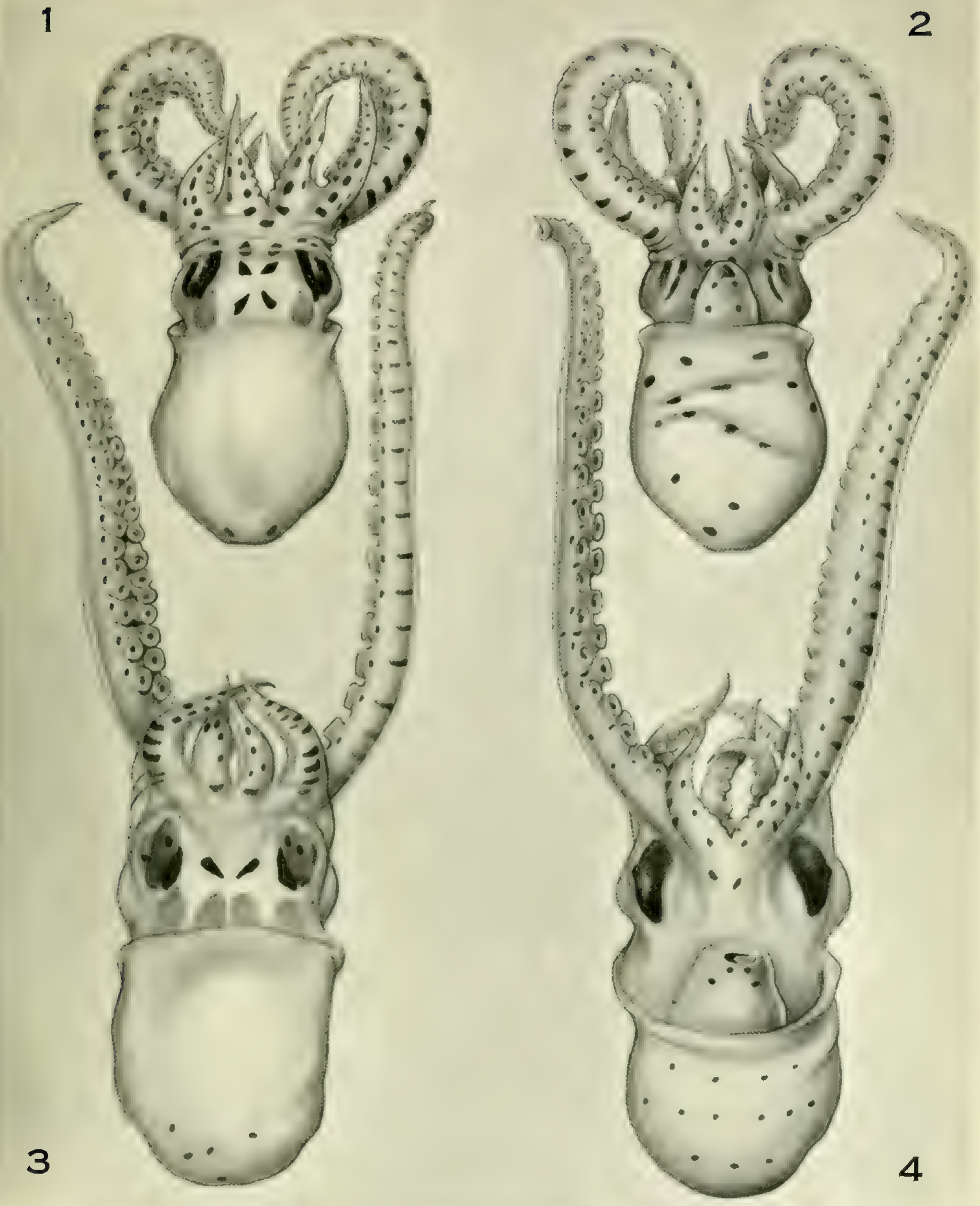
PLATE 3.

FIGS. 1 and 2. *Macrotritopus* larva of 3·45 mm. in ventral mantle length from "Discovery" St. 2646.

FIGS. 3 and 4. *Macrotritopus* larva of 3·75 mm. in ventral mantle length from "Discovery" St. 276. This specimen was taken in the same haul as Robson's syntypes of *M. kempi*.



MACROTRITOPUS LARVAE.

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HEARING IN CETACEANS

PRESENTED
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F. C. FRASER
AND
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BULLETIN OF
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ZOOLOGY Vol. 2 No. 5
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HEARING IN CETACEANS

By F. C. FRASER AND P. E. PURVES.

SYNOPSIS

Essential anatomical features of the region of the ear of cetaceans are described and figured.

Earlier hypotheses relating to the mode of hearing in cetaceans are briefly reviewed and criticized.

Reasons are given for regarding the method of hearing in cetaceans as being essentially similar to that of terrestrial mammals with certain anatomical modifications required for receiving water-borne vibrations.

A simple experiment is described demonstrating the superiority of the walls of the meatus over other parts of the body as a conductor of longitudinal vibrations.

At the present time the sounds emitted by cetaceans and consequently their sense of hearing are the subject of a considerable amount of investigation. The remarks that follow are in anticipation of a more detailed account of the cetacean ear which the writers have in preparation.

In order to clarify the hypothesis arrived at a brief summary of the anatomical features involved is necessary (in connection with which reference to Plates 1 and 2 should be made).

The external auditory meatus is a continuous narrow tube in the toothed cetaceans (with the exception of *Physeter catodon*, see Clark, 1948). In the whalebone whales it is usually closed for some part of its length immediately internal to the blubber layer. The meatus is lined by a pigmented extension of the epidermis. Surrounding the lining layer is a fibro-elastic sheath, the fibres of which run predominantly along the length of the meatus. Surrounding this sheath again is a fibro-cellular structure in which a thin stratum of circular constrictor muscle has been observed.

Associated with the tube are incompletely investing cartilages into which auricular muscles are inserted. Of these one of the most important is the m. auricularis-occipitalis-profundus which Bonninghaus (1904) described and figured in detail in connection with the dissection of a Common Porpoise. Bonninghaus' figure shows the acute dorsally- and slightly caudally-directed bend into which the meatus is thrown in its course. The muscle just referred to originates at the top of the skull and extends downwards to its insertion at the apex of the bend in the meatus. Another equally important muscle is Bonninghaus' m. zygomatico-auricularis which has its origin on the zygomatic process of the squamosal and converges to be inserted into the cartilage at the inner end of the meatus.

In both toothed and whalebone whales the meatus widens out mesially to terminate at the tympanic membrane. The latter is not as in terrestrial mammals a thin translucent membrane. It consists of two parts, a fibrous region containing radial and concentric fibres and a fibreless region similar to the pars flaccida of land mammals. The fibrous portion consists of a broad flattened triangular " ligament " with one edge of its base attached to part of the tympanic ring, the base thus forming part of the external surface of the " membrane." The attenuated apex of the " ligament " formed by the convergent radial fibres is directed mesially and is attached to a small process on the manubrium of the malleus. It is this ligament[1] which, in the opinion of the writers, is the true homologue of the fibrous portion of the tympanic membrane of land mammals. The non-fibrous portion bridges the space between the fibrous portion and the remainder of the tympanic ring. In *Phocaena phocoena* (*fide* Bonninghaus) the non-fibrous portion merely forms a few islets in the fibrous portion ; it is single and more extensive in area in the *Globicephala melaena* specimen examined by the writers and in their opinion the " glove finger " of the whalebone whales, described by Beauregard (1891) and Lillie (1910) as well as by earlier anatomists, is the same structure very greatly enlarged.

The three auditory ossicles commonly found in the Mammalia are also represented in the Cetacea. In the latter the malleus is fixed by the processus gracilis to the margin of the tympanic annulus at the position of the Glaserian cleft. This condition is not peculiar to cetaceans, Hyrtl (1845) and Bonninghaus (1904) having described it in monkeys, carnivores and insectivores. The hammer-shape is maintained but it is the processus gracilis which resembles the handle. The head, in addition to the portion recognized as such in other mammals, includes the manubrium, which is very much reduced in length to form a short tubercle. The processus gracilis is longer and stouter than that of other mammals and in structure somewhat resembles a short length of channel girder. At the junction of the malleus with the Glaserian cleft the tympanic ring is developed into a strong wing-like lateral projection buttressed to the processus gracilis. This projection known as the sigmoid process is peculiar to the Cetacea, and plays an important part in the mechanics of the cetaceans' hearing.

The head of the malleus is deeply notched by two large facets making a re-entrant angle on its posterior aspect. Both of the facets have smooth, shallowly convex surfaces covered with articular cartilage which with the corresponding facets on the incus form part of a synovial joint. The radii of the convexities, as well as that of the arcuate junction between the two facets, lie approximately at right angles to the long axis of the tympanic ligament.

The tensor tympani muscle, which appears to be largely tendinous, is attached to the ventral wall of the periotic near that part of the tympanic cavity associated with the outlet of the Eustachian tube. Although in its course to the malleus it is directed meso-laterally approximately in line with the long axis of the tympanic ligament, the attachments of the muscle and tympanic ligament to the malleus are displaced dorso-ventrally from one another by a small distance. The ligament and muscle are not antagonistic to each other but form a mechanical couple.

The form of the incus is comparable with that of mammals generally. The facets for articulation with the malleus are shallowly concave, furnished with articular cartilages and meet at an angle which fits into the re-entrant angle of the malleolar facets. The processus brevis is a short conical projection directed anteriorly. The ligament attaching the incus to the periotic bone, the axis of the processus brevis and the lateral margin of the processus gracilis make a common axis.

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[1] It will be referred to as the tympanic ligament in this paper.

The stapes departs so little from the normal that its description is unnecessary, but it should be mentioned that, contrary to the statements which have been made that the foot is fused to the periotic at the fenestra ovalis, no evidence of this could be found by the present writers. It is probable that the impression of fusion is due to the perfect fit of the foot in the fenestra ovalis.

The tympanic bulla, the general form of which is sufficiently well known not to require detailed description, may be said to have a mesial and a lateral portion which meet ventrally in a roughly semi-circular ridge and are separated dorsally by the cavity of the bulla. The mesial part is characterized by its stout petrous nature (the bone in rorquals being up to 3–4 cm. thick), and by the smoothness of most of its surface, both of these features are associated with its contiguity with the air sinuses. The lateral portion is much thinner, and has a roughened outer surface, these features being associated with its contiguity with the surrounding fibrous layer, which is about 12 cm. thick in a large rorqual and strongly adherent to the lateral surface of the bone. The bulla in the whalebone whales is attached by two thin, flat pedicles placed respectively anteriorly and posteriorly and having their planes approximately at right angles. The cavity of the bulla is continuous with that of the middle ear and its associated air sinuses. In the Odontocetes the anterior pedicle is absent and the posterior support does not involve bony fusion of the tympano-periotic junction.

In all cetaceans the periotic is separated from the rest of the skull at the squamo-mastoid boundary. In the rorquals the much attenuated mastoid process is loosely wedged between the squamosal and basi-occipital bones—being maintained in position by fibrous tissue. The mastoid process of the beaked whales and some River Dolphins is less attenuated but much convoluted—the convolutions interdigitating with corresponding cavities on the postero-ventral tip of the squamosal. There is no fusion of the bones.

In the Delphinidae the periotic is neither wedged into, nor interdigitated with, the squamosal, but is separated from the bones of the cranium by an appreciable gap. Between the mastoid process—which is very short—and the basi-occipital there is a fibrous ligament which appears to be the only well defined point of attachment to the skull.

The cochlea and semi-circular canals occupy only a relatively small part of the petrous bone as a whole. It has been stated that in cetaceans the laminae spiralis primaria and secondaria of the cochlea make a continuous bony septum across the spiral labyrinth. The authors' dissections show that this is not so and that whilst the gap between the two laminae is very narrow at the entrance to the scalae it gradually widens towards their apex. There is a basilar membrane and organ of Corti as in other mammals. In all but absolute size the cochlea conforms with the usual pattern.

The cavity of the middle ear communicates with the Eustachian tube and with a system of pneumatic sinuses which in volume, extent and structure are peculiar to the cetaceans.

In the region of the auditory organ accessory air sinuses occupy the space between the mesial aspect of the periotic and the surrounding bones of the skull as well as separating the periotic from soft parts on its lateral aspect.

Anterior to the tympanic bulla a very large air sinus is developed which in the rorquals occupies nearly the whole of the pterygoid fossa. In the beaked whales and dolphins this sinus is even more extensive and covers the greater part of the base of the cranium in addition to the pterygoid fossa, which is very much enlarged. In the Common Dolphin this sinus has an anterior extension which passes forwards on the ventral surface of the rostrum for approximately two-thirds of the latter's length.

The mesial walls of the pneumatic sinus are closely applied to the bones of the skull. Laterally and externally the sinuses are closed by a tough, fibrous membrane resembling periosteum to which some of the muscles of the lower jaw and palate are attached. A comparative study of this membrane shows that in the more primitive species it overlies thin sheets of bone and it has been suggested that the enclosed sinuses are the homologues of the pneumatic sinuses found in the skulls of terrestrial mammals (Monro, 1785).

Within the fibrous closing membrane there is a fibro-venous plexus which extends over the whole of the inner surface of the air sinuses. The plexus is made up predominantly of large vessels which appear flattened when the sinuses are injected with air or other media but become turgid when injected themselves under pressure. In this state they obliterate the cavity of the air sinuses. Lining the latter and covering the inner aspect of the fibro-venous plexus is a thick mucous membrane which is continuous with that of the middle ear and Eustachian tube and is remarkable for the richness of its glands and ducts. The openings of the ducts, which cover the entire inner surface of the air sinuses, are less than ·1 mm. apart and lead into a maze of smaller racemose channels and crypts lined with columnar epithelium and goblet cells.

At the entrance to the ducts and on the exposed surface of the mucous membrane is a layer of ciliated epithelium. The writers' observations, and those of Brazier Howell (1930) on freshly killed specimens reveal that the sinuses are entirely filled with an albuminous foam. Whether this is so in living animals cannot be ascertained, but the anatomical evidence suggests that it is.*

The Eustachian tube diverges from the general air cavity at a point just anterior to the tympanic bulla—and passes forwards for a short distance along the mesial aspect of that part of the sinus which goes to occupy the pterygoid fossa : thereafter it passes upwards and gradually narrowing, opens into the nasopharynx. Its closing walls are made up of fibrous tissue and a fibro-venous plexus similar to, and continuous with, that of the air sinuses. The lining mucous membrane is deeply indented with valvular pockets and folds which are directed towards the choanae.

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* Additional evidence of foam in the air sinuses has been received from Mr. D. E. Sergeant, Newfoundland Fisheries Research Station, St. John's, Newfoundland, who writes (10-8-53): "*Globicephala melaena*, female, 9′ 6″ in length, dead about 1½ hours. Anterior region of sinus within pterygoid exposed by means of saw cuts ; seen to be filled with foam".

The fibro-venous plexus referred to above is supplied by an arterial plexus which emerges from the external maxillary artery immediately anterior to the tympanic bulla, and by small arterial branches which emerge from the same artery as it passes forwards across the ventral surface of the cranium. The plexus is drained by three distinct paths :

> (1) By large vessels which communicate with the transverse and cavernous sinuses of the cranium and drain eventually into the spinal-meningeal veins.
>
> (2) By large vessels which join the external jugular vein via the vena pterygoidea.
>
> (3) By an intricate plexus of small veins which penetrates the fibrous covering of the sinus at the angle formed by the lateral pterygoid and the tensor palati muscles. This plexus is very dense and ramifies throughout the mass of fatty tissue which lies on the mesial aspect of the lower jaw—eventually coalescing into a single vessel which joins the external jugular vein.

The aquatic environment of whales and the extreme narrowness of their external auditory meatus have led most students of cetacean anatomy since Camper (1767) to search for some mode of hearing other than that which is normal for terrestrial mammals. Camper's hypothesis was to the effect that cetaceans could only hear when lying quietly at the surface with the external aperture of the meatus out of water. Hyrtl (1845), who recognized that whales must be able to hear well under water, held the view that while the external meatus was unsuitable for the reception of air-borne sound waves, it was suitable for the reception of " waves of compression " such as are transmitted in water.

Buchanan's (1828) belief was that sound was conducted to the tympanic membrane by way of the Eustachian tubes. This view was criticized by Claudius (1858) on the ground that the Eustachian tubes are normally closed while the cetacean is submerged. Claudius' own view was that the water-borne sound vibrations were taken up by the bones of the skull, transmitted to the pneumatic sinuses, thence to the auditory ossicles but principally to the membrane of the fenestra rotundum which he regarded as the main oscillator of the cochlear fluid. Turner (1913) agreed with Claudius' interpretation. Bonninghaus (1902) invoked the pinna-like shape of the anterior portion of the tympanic bulla as a collector of sound waves ; vibrations which he terms " molecular " are transmitted by way of the processus gracilis through the ossicles to the fenestra ovalis.

Lillie (1910) says "the whale probably receives sound vibrations by means of vibrating bony surfaces, after the manner of fishes. The tympanic bulla is a relatively dense and heavy sounding-box, fastened to the periotic bone by two thin pedicles, so that it could easily be set in vibration. The bulla is connected with the fenestra ovalis by the chain of ossicles, the auditory apparatus being thus independent of the tympanic membrane." Kellogg (1938) concurred with this view.

In the opinion of the present writers Hyrtl's interpretation is the most acceptable one. The anatomical features of the cetacean ear, far from indicating that cetaceans hear by abnormal means, support the view that the mode of hearing is essentially as in land mammals with precisely those modifications of structure which are required for receiving water-borne vibrations.

Any working hypothesis relating to hearing in cetaceans must be based on the assumption that these animals have the same requirements as terrestrial mammals. These requirements are that hearing should be directional, discriminative, selective and anticipative. The accepted hypotheses for directionality in hearing involve an appreciation of an intensity and/or phase difference in the sounds received by the two essential organs of hearing respectively. On the face of it it is difficult to see how this can be achieved by bone conduction.

In the binaural reception of sound necessary for directionality the advantages of the cochlea being situated at or near the extreme lateral limits of the skull are offset by the likelihood of mechanical damage and extreme limitation of voluntary controllability of the sounds entering the external opening of the meatus. The muscularly controlled pinnae of land mammals enables them, in addition to securing directionality, to control the volume of sound received. In the Cetacea the anatomical evidence indicates that binaural hearing is achieved by placing the two receptors remote from the surface of the body, by isolating them acoustically from the rest of the body and each other, and by connecting them to the surface of the body laterally by an apparently acoustically efficient muscularly-controllable vibration conduit. The acoustic isolation of the periotic is achieved by (1) its dissociation from the adjacent bones of the skull, (2) the provision and maintenance of an air gap between it and the rest of the skull at all hydrostatic pressures, (3) the foam which, on the evidence of freshly-killed animals, appears to occupy the air sacs and middle ear of the living animal. The first of these has already been described. The second is achieved by the mechanism of the accessory air sinuses. As the hydrostatic pressure increases with depth the blood is forced into the venous plexus lying below the fibrous outer covering of the sacs. The volume of the air sacs is correspondingly reduced and the compressed gas is contained in the rigid tympanic cavity and in the space between the periotic and skull. With diminishing depth the process is reversed. This interpretation of the function of the air sacs agrees with that put forward by Beauregard (1891) except that the role of the venous plexus does not coincide with his view.

Owing to the flattening of the large lining veins when the air sinsues are inflated the blood drainage from the venous plexus and mucous membrane must be predominantly through the rich plexus of small vessels which passes through the mass of adipose tissue occupying mesial concavities of the lower jaw. The very close association of the plexus with the fatty tissue and the known high nitrogen absorption capacity of the latter compared with that of blood (6 : 1) suggest that the fat may play a part in the absorption of nitrogen contained in the pneumatic sinuses. That the mucous membrane of the sinuses may have a gas-secreting function is a possibility which requires further investigation.

In considering the theory expressed by Claudius and implied by Bonninghaus that sound waves are conveyed to the tympanic bulla through the air in the pneumatic sinuses it must be pointed out that films of air surrounded by media of high acoustic resistance like water do not transmit sound well. For example, a film of ·1 cm.

of air surrounded by water reflects about 93% of the incident energy of a sound wave of 1000 c.p.s. (Wood, 1941). If the air is surrounded by solid rock or presumably by a substance equally hard, for example, petrous bone, the reflected energy is about 99·93%. If in addition the air cavity is filled with foam the reduction in energy would be even greater.

The efficiency of the bubbles in damping vibrations increases rapidly both as their diameters and distance apart diminishes, thus in the cetacean as the animal dives the acoustic isolation could be maintained in spite of the reduction in volume of the foam-filled cavity.

In view of this apparent acoustic isolation of the essential organs of hearing it was decided to examine the external meatus as a possible vibration conduit. Claudius states that "All true cetaceans toothed as well as whalebone possess absolutely no functioning ear passage" and subsequently after a very incomplete description of the meatus states " The cord is then, neither homogeneous nor taut, and its conducting power very slight, and by no means any greater than that of the surrounding fat layer." The anatomical and experimental investigations carried out by the writers do not support Claudius' conclusions, but point to a set of conditions which are exactly the reverse.

The lining walls of the meatus appear extremely homogeneous (*vide supra*) and the arrangement of the two most conspicuous auricular muscles would appear to be precisely that necessary for maintaining either or both auditory conduits in any state of tension required.

In order to obtain some indication of the sound conductivity of the meatus relative to that of adjacent tissues a simple test was made. For the mechanical vibrations required the output of a variable frequency oscillator (30–10,000 c/s) was connected to the input of an amplifier of a loud speaker. A loop of dental floss was attached to the centre of the loud speaker and the two ends attached to two small pieces of perforated zinc which had been stitched to the wall of the meatus and the adjacent fibrous tissue respectively. The specimen used consisted of a large piece of the squamo-occipital region of the head of a Fin Whale which, deep frozen while fresh, had been defrosted and dissected to expose the tympanic cavity.

For indicating the relative strength of received vibration signals a gramophone pick-up was connected to an amplifier, the output of which was connected to a rectifying millivoltmeter.

With a fixed output from the oscillator and with the pick-up needle placed at the external end of the meatus, the input potentiometer of the amplifier in the pick-up circuit was adjusted to give a reading of 0·4 mv. at the millivoltmeter. To obtain the same reading with the pick-up needle placed at the malleolar end of the tympanic ligament the input potentiometer of the amplifier had to be adjusted. This adjustment corresponded to a voltage ratio of 10 : 1 so that assuming that the voltage reading is directly proportional to the mechanical vibration picked up, the signal received at the malleolar end was about 1/10 that applied at the outer end. When attempts were made to pick up signals on the periotic bone, on adjacent skull bones, on the muscular or on the fibrous tissue in the neighbourhood of the tympanic cavity the millivoltmeter reading fell to zero. With the apparatus available for this simple test the limits set by the oscillator output and the amplification in the pick-up circuit, prevented a quantitative comparison being made between these last tests and the first one. The indication is, however, that the signal in any case is less than a quarter of that obtained at the malleolar end of the tympanic ligament.

The results confirmed earlier preliminary tests made with a stethoscope. Because of the mechanical difficulty of placing the stethoscope on the malleus the vibration was applied to the point of attachment of the tympanic ligament and the signal picked up at the external end of the meatus. With this arrangement good signals were received, but with the stethoscope applied to surrounding tissues results were negative.

To satisfy the discriminative condition it must be assumed that the cetacean cochlea is as selective as that of terrestrial mammals. Certainly its general anatomy suggests that this is so. The physical properties of water-borne vibrations, however, differ markedly from those which are airborne. The pressure-amplitude for the same intensity and frequency of water and air-borne sound is in the ratio 61 : 1, and the displacement amplitude 1 : 61. The mathematical treatment of the subject is not within the scope of this paper but it can be shown that adjustments of amplitude and pressure to values normally experienced in the cochlea by terrestrial mammals are probably achieved in cetaceans by the modifications of the malleus and incus.

Before describing the functioning of the cetacean ossicles it is necessary to repeat the often quoted modus operandi of the human ear. The following is from Gray's *Anatomy* (1946) :

> " The handle of the malleus follows all the movements of the tympanic membrane, while the malleus and incus rotate together about an axis which runs through the short process of the incus and the anterior ligament (and therefore the processus gracilis) of the malleus. When the tympanic membrane and handle of the malleus move inwards the long process of the incus also moves in the same direction and pushes the base of the stapes towards the labyrinth."

A mechanical study of their ossicles shows that the foregoing description is true for cetaceans with one important difference. In man and other terrestrial mammals the long axis of the malleus is parallel with the plane of the tympanic membrane and the manubrium is firmly attached to the latter as far as its centre. Thus the amount of movement of the centre of the tympanic membrane is identical with that of the tip of the manubrium. In cetaceans the membrane (i.e., the tympanic ligament) is attached only to a point at the tip of the manubrium of the malleus. The attachment to the tip is so situated that a line through the centre of the tympanic ligament is parallel with the long axis of the manubrium. This means that any small movement of the meatal end of the tympanic ligament produces a relatively large movement of the tip of the manubrium and therefore of the tip of the long process of the incus. In order that this amplification be produced the effective movement of the malleus must be solely rotational and this is achieved by the stout channel-girder construction of the processus gracilis and its firm fusion to the tympanic ring. In addition, its lateral edge is strongly buttressed by the sigmoid process of the tympanic ring. This construction ensures that lateral movement of the malleus is obviated and that the processus gracilis is capable of torsional vibration only. The angular articulation of the malleus with the incus produces a condition in which there is positive oscillatory drive by rotation only. The smooth curved surfaces of the facets tend to slip over one another in one or both directions when the oscillation is transverse or longitudinal to the processus gracilis. This factor must be of great importance in the exclusion of extraneous vibrations. In this last connection it is necessary to examine the hypothesis of Lillie and Kellogg (*v. supra*) in more detail and as a preliminary it will be useful to recall Beauregard's (1894) conclusions on the subject.

> " The tympanic bulla cannot be regarded as an apparatus for resonance as has been asserted by various anatomists and physiologists (Hunter, Home, Esser, etc.). The massiveness of the walls of the bulla and its shape recalling more or less that of a shell have evidently given birth to this idea, but the facts do not justify it. These so-called resonators are more or less completely enveloped by soft parts which do not favour their action. The shape is extraordinarily variable in reality and the massiveness of the walls is necessary to obtain a rapid equilibrium of pressure between the air which fills the bulla and that of the exterior. Savart was therefore correct in saying that the tympanic cavity has the function of retaining near the entrance of the labyrinth and on the internal aspect of the tympanic membrane an atmosphere of which the physical properties are constant."

In agreeing with this view the writers would draw attention to additional anatomical details which support it. (1) the great thickness and strength of attachment of the fibrous capsule which envelops the ventro-lateral aspect of the bulla, this being the part which would be most easily thrown into vibration ; (2) the extreme density and thickness of that part of the bulla which is exposed to air on both surfaces, the internal damping of such a mass must be considerable ; (3) the angular set of the two thin pedicles is such that the bulla would not easily be thrown into vibration, but assuming it were it would be expected to vibrate about an axis running through the pedicles. Examination of the positioning of the articular facets of the malleus in relation to this axis indicates that no drive to the incus could be achieved (the connection between the malleus and incus has already been described).

The majority of sounds in water can be regarded as being conveyed from a point source by spherical pressure waves. When such waves impinge on the cetacean body, and assuming the least favourable acoustic conditions, i.e., that the general shape and various tissues of the body are non-reflecting, the body mass would form no barrier to the progress of the waves except in the neighbourhood of the ear. Here the sound energy, except that conveyed by the external meatus, must undergo almost complete reflection because of the gaseous content of the tympanic cavity and accessory air sinuses. The walls of the external meatus would be thrown into longitudinal vibration whether or not a continuous free lumen existed. Such vibrations would be conveyed to a point on the mesial end of the manubrium mallei by the convergent fibres of the tympanic membrane. The oscillations of the malleus thus initiated would be conveyed to the cochlear fluid over the bridge formed by the auditory ossicles.

In terrestrial mammals the intensity of sounds received can be governed by orientation of the head, but principally by the use of auricular muscles. In the Cetacea the orientation of the head in relation to the rest of the body is limited by the absence of a well-defined neck. If, however, it is accepted that the sounds received at the cochlea of the cetacean are conducted along the external auditory meatus by longitudinal waves the degree of tension of the walls of the meatus must be a controlling factor in sound intensity. The m. auricularis occipitalis profundus and the m. zygomatico-auricularis of the Porpoise described by Bonninghaus seem particularly well suited in position and structure for the function of adjusting the tension. The meatus, however, is attached to the tympanic annulus and an additional mechanism is required to maintain the tension of the fibrous portion of the tympanic membrane lying within the tympanic cavity. The positioning of the non-fibrous portion of the membrane in relation to the fibrous portion is such that under the influence of the gaseous pressure within the tympanic cavity the necessary tension could be provided. The final expression of this function can be seen in the " glove-finger " of the rorquals. In them the non-fibrous portion is enlarged in correspondence with the greatly elongated tympanic ligament.

The arrangements which exist in terrestrial mammals for making small temporary adjustments to the tension of the tympanic membrane are also present in the Cetacea, but in view of the coarse adjustment required it is doubtful whether the tensor tympani muscle is as effective in this respect as it is in terrestrial mammals. The palatal and lateral pterygoid muscles are however very well developed in cetaceans and their relationships to the Eustachian tube and pneumatic sinuses suggest that they may play an important part in the adjustment of the gaseous pressure within the tympanic cavity and consequently of the tension on the tympanic ligament.

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Munesato Yamada's " Contribution to the Anatomy of the Organ of Hearing of Whales," reprinted from the *Scientific Reports of the Whales Research Institute*, No. 8, 1953, was received after completion of the foregoing preliminary account. It will be considered in the more detailed paper which the authors have in preparation.

EXPLANATION OF PLATES

PLATE 4

FIG. 1.—Dissection to expose the ventral aspect of the left ear of a Pilot Whale, *Globicephala melaena.* Cut surfaces of bone hatched and the corpus cavernosum shown reflected. Abbreviations used in this and the following figures :—

AAS —Accessory air sinus.
AC —Auricular cartilage.
AL —Anterior ligament.
AP —Anterior pedicle.
B —Blubber.
C —Cochlea.
CC —Corpus cavernosum.
EAM—External auditory meatus.
FO —Fenestra ovalis.
FR —Fenestra rotundum.
FVP —Fibro-venous plexus.
GL —Glove finger.
I —Incus.
LI —Ligamentum incudis.
M —Malleus.
MM —Manubrium mallei.
OC —Occipital condyle.
P —Periotic.
PG —Processus gracilis.
PP —Posterior pedicle.
PTS—Pterygoid sinus.
S —Stapes.
SC —Semicircular canal.
SM —Stapedial muscle.
SP —Sigmoid process.
TA —Tympanic annulus.
TB —Tympanic bulla.
TL —Tympanic ligament.
TT —Tensor tympani muscle.

FIG. 2.—Detail of figure 1.

PLATE 5

FIG. 1.—Dissection to expose the ventral aspect of the left ear of a foetal Lesser Rorqual, *Balaenoptera acutorostrata.* (Abbreviations as for Plate 4, figure 1.) Corpus cavernosum shown reflected.

FIG. 2.—Right tympanic annulus and auditory ossicles of a Humpback Whale, *Megaptera novaeangliae.* The dotted line indicates the axis of the tympanic ligament. (Abbreviations as for Plate 4, figure 1.)

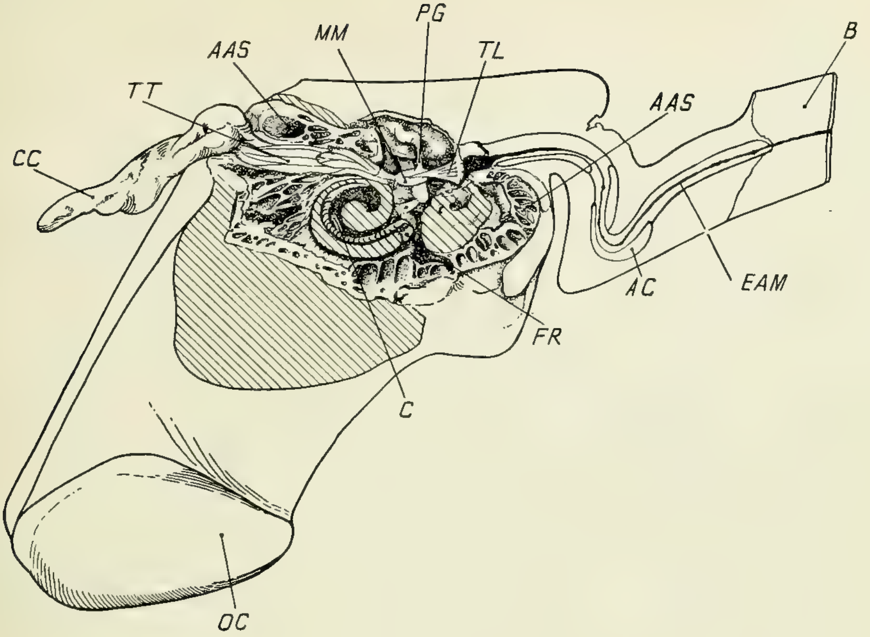
PG
MM
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FIG. 1.

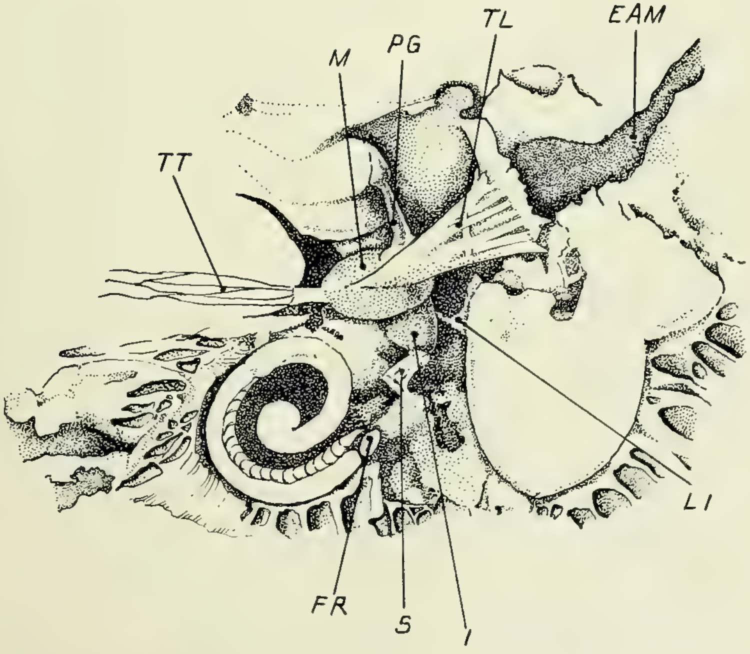
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FIG. 2.

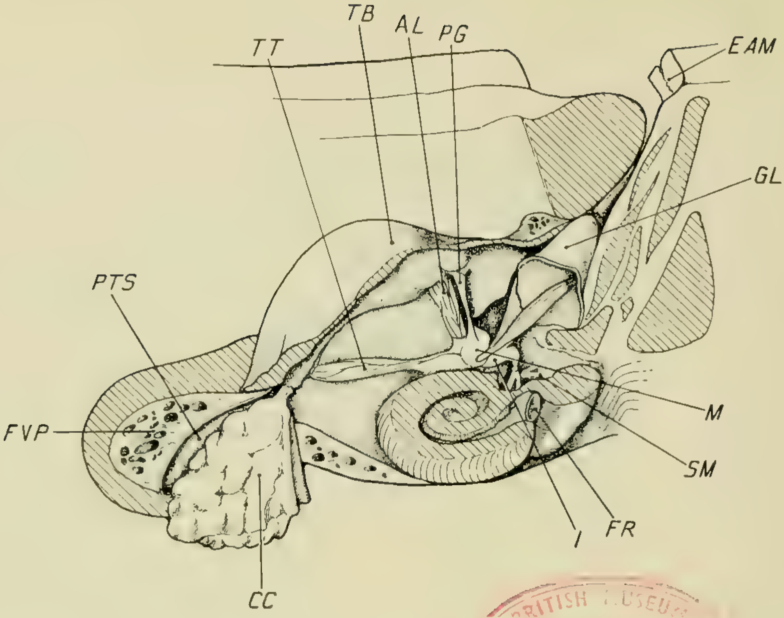
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FIG. 1.

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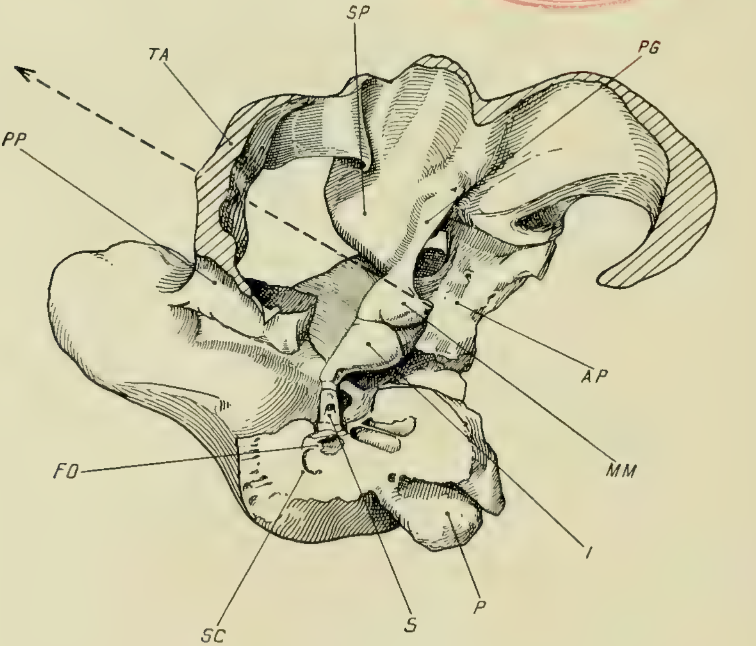
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FIG. 2.

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THE "ROSAURA" EXPEDITION

BULLETIN OF
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ZOOLOGY Vol. 2 No. 6
LONDON: 1954

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THE "ROSAURA" EXPEDITION

1937-1938

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FOREWORD

The collections made by Mr. J. S. Colman during the cruise of Lord Moyne's yacht " Rosaura " in the north and central Atlantic and the Caribbean region were received at the British Museum (Natural History) only a short time before the outbreak of war. In consequence little work was done on them at the time, and during the post-war years there have been many tasks of greater urgency. In some groups the material collected adds little to existing knowledge and no special report on it, as a whole, is warranted. In such instances new knowledge has been, or will be published elsewhere; published papers dealing with " Rosaura " material are listed by Mr. Colman in the bibliography attached to his narrative of the cruise (p. 130).

The present Bulletin contains a random collection of reports at present available. Others may be expected from time to time in this Bulletin.

1. GEAR, NARRATIVE AND STATION LIST

By JOHN S. COLMAN.

IN 1937 Lord Moyne took his yacht " Rosaura " on a long cruise in the North Atlantic and decided to add deep-sea collecting to the other activities of the trip. I was fortunate to be taken on as zoologist.

We left Southampton on 21st August, 1937, and returned there on 6th February, 1938, after covering 18,565 miles. We called at the Scilly Isles on the way out, and then proceeded straight to Angmagssalik in East Greenland, where we spent four days. We then rounded Cape Farewell to Julianehaab, the capital of southwest Greenland, and visited several fjords in the neighbourhood. Next we had to double back to St. John's, Newfoundland, in order to fit new propellers in the dry-dock there, as ice had removed a blade from the port propeller in Angmagssalik harbour. This prevented a projected run up the west coast of Greenland to Disko, so instead we went from St. John's to the Labrador coast. In southern Labrador the harbours are not good, as the low, smooth hills afford very little protection from the wind, and the bottom is often hard and poor holding-ground ; we dragged our anchors in two successive " harbours " and had to put to sea each time. After Labrador we visited three of the fine inlets on the west coast of Newfoundland and then proceeded to Cape Breton Island, where " Rosaura " was again forced to go out to sea when the wind freshened ; this, however, was the last heavy weather we had on the entire cruise.

The first part of the voyage ended at New York ; our route was then *via* Charleston, Nassau, Cap Haitien in Haiti, Jamaica, Grand Cayman, Swan Islands and the Bay Islands of Honduras, to Belize in British Honduras. The Bay Islands and Swan Islands turned out to be unexpectedly interesting, the latter biologically and the former by providing enormous quantities of pottery which is probably pre-Columbian, so we revisited them before running south to Colon on the Panama Canal. From here the course was by the San Blas Archipelago of Panama to Puerto Cabello and La Guayra in Venezuela, then by Grenada, Tobago, Little Tobago and Trinidad to Demerara and the Barima River, and on to Para. Christmas was spent in Pernambuco, after which a visit was paid to St. Paul's Rocks on the way across the Atlantic to the Gambia River, up which we went for 120 miles. We then had an exasperating three weeks in Dakar with two visits to the dry-dock, but we thereby missed two severe January gales off the English Channel, and ourselves had almost a glass calm from Finistere to Southampton. The whole cruise was described by Lord Moyne in *Atlantic Circle* (Blackie 1938).

" Rosaura " was a vessel of some 1,500 tons, 282 feet long and drawing about 12 feet of water. (She was lost during the 1939–1945 war). She started life as the cross-channel steamer " Dieppe " and was converted from steam turbines to diesel engines, but the lighting, heating and capstans were still worked by steam. I mention this because the chief piece of collecting equipment was the steam winch off R.R.S. " Discovery I," which could thus be built into " Rosaura " with the minimum of alteration. This winch had some 3,500 fathoms of wire and did its work splendidly, giving very little trouble. The only place for it was on the deck just forward of the bridge, and this proved to be the best possible position, for two reasons. First of all, the most practicable lead for the wire was then over the bows, and this meant towing with the engines going astern ; going slow ahead on one engine " Rosaura's " minimum speed was 3 or 4 knots, but going astern this could be reduced to 2 knots, about right for plankton work or for dredging. Secondly, " Rosaura " had a very strong idiosyncracy, that of always trying to lie stern to wind ; this made towing over the bows a simple matter, and sometimes neither the wheel nor the engine-room telegraph had to be touched during the hour or more that the net was towing.

For work on the bottom we had a 10-foot Agassiz trawl and dredges 2 and 3 feet across. The Agassiz trawl was on the whole very successful and only came to grief once, when we tried a trawl in 1,000 fathoms off Swan Islands ; about 70 fathoms of wire came up in a knot with the cod-end of the net in the middle ; the deepest successful haul was from 700 fathoms near the Canaries.

Occasions for deep bottom trawling were limited by the scarcity of suitable depths (1,000 fathoms was about our maximum), so the bulk of the collection consists of deep-sea plankton from between about 700 fathoms and the surface, caught in a stramin net with a diameter of 2 metres. Since we did not have closing apparatus, the net was sent down and hauled in open. It was towed horizontally for an hour, or sometimes more, in deep water, and then took about half an hour to heave in, so the catches must contain a good deal of material from the upper layers and the surface. In addition I made several coastwise and estuarine hauls with a small silk tow-net 50 cm. in diameter.

All the nets and frames were obtained from the Plymouth laboratory of the Marine Biological Association, where they were made exceedingly well and with remarkable speed, and the British Museum supplied jars, tubes, formalin and alcohol, of which last I used 45 gallons. Every haul was sorted and bottled off at once unless the ship was rolling too heavily. A plankton haul would take a day and a half and a dredged haul from one to three days, as the sorting was done in fair detail, particularly in the more abundant groups such as mollusca and crustacea.

It was too rough to do any work on the way over to Greenland, so the first collecting was done in Angmagssalik harbour. The bottom is rather like the surrounding mountains, which are steep and rugged, and the harbour has not been charted, so we dredged from a motor-boat close to the rocks where we could find bottom in 20–30 fathoms. Although the depth was altering constantly the bottom was of mud, at any rate in places, and it was extraordinarily rich in life. There were 14 species of bivalves, about as many of Polychaetes, many algae and many crustacea, but curiously enough no crabs. Crabs seem to be rare in Greenland, for in five dredge-hauls and shore-collections I caught only two in all. Otherwise the Greenland marine fauna and flora are both remarkably rich, but are on the whole not easy to come at. In places like Angmagssalik harbour the sea floor is extremely uneven, so much so that one night when " Rosaura " was shifting her moorings during a gale the echo-sounding gear showed every depth from 14 to 70 fathoms and back again in under a quarter of a mile ; then, again, over the coastal shelf the sea-room necessary for fairly deep trawling is strictly limited by the proximity of icebergs, and the bottom is so foul with glacial boulders that a long haul is bound to result in the loss of some part of the gear. A canvas sock outside the net is absolutely essential. Our one successful bottom-haul off Greenland, Station 6, brought up large numbers of brachiopods, bivalves, polychaetes and ophiuroids ; the coastal plankton also contained many ophioplutei, so that brittle-stars may be a dominant group in these parts.

On leaving Greenland we made for St. John's, Newfoundland, to fit spare propellers as the ice had broken a blade off the port propeller while we were anchored at Angmagssalik. On the way we tried out the 2-metre stramin net for the first time, and rather rashly did so at night. It was a most instructive station, as nearly everything happened except the loss of the net or of the catch. We could not use the port engine, the sea was not running true with the wind and " Rosaura " accordingly lay rather across the sea, rolling heavily, and to crown all the West Greenland current kept driving the ship over the wire. Sometimes the wire paid off ahead as it should, sometimes it grew straight up and down, and twice it went right under the keel and paid off astern on the starboard side. Finally a davit-guy parted but this was countered with a jury tackle from the anchor davit, and eventually the net was brought aboard. Rather to our surprise it contained a rich and very phosphorescent catch, including some eight or ten species of scypho-medusae—more than at any other station. This catch was more phosphorescent than any other, probably because it was the only deep plankton haul made where the surface water was cold.

In St. John's harbour there were many patches of red water which gave quite a distinctive appearance to the inlet. They were caused by myriads of cladocera, each containing a yellow drop of oil.

St. John's welcomed us with an unprecedented heatwave at 92° F., but after we left for Labrador we were told the same thing wherever we went for a fortnight—" What a pity you weren't here two days ago ; this is the first foul weather we have had for months !" This weather limited collecting opportunities on the Labrador coast, and we could not even remain in harbour, as I have mentioned, since the holding-ground was so poor. I did get in a dredge haul from the dinghy between two gales (Station 10), and so found out what the charts mean by describing the bottom as " coral " over so much of this coast. The net came up entirely filled with a branching coralline alga, which evidently covers large areas of a rocky bottom and is itself very hard. It acts like roller-bearings under the flukes of a boat's anchor and must make the holding-ground even worse than bare rock.

We came south down the west coast of Newfoundland and tried out the Agassiz trawl in Bonne Bay. This is an inlet with only 6 fathoms at the mouth, but with 120 fathoms further in where we trawled ; there is no similar depth nearer than forty miles out in the Gulf of St. Lawrence. The bottom of Bonne Bay is of mud, with some stones and a good deal of waterlogged lumber. More than half the animals were ophiuroids in prodigious numbers, but most of the main groups were represented and the collection was unusually varied for such a muddy bottom. Three large scarlet anemones were rather unexpected, but these appear to have a foot specially adapted for living in mud; the lower end of the body is solid and hemispherical, and surrounded by a wide and muscular frill; the anemones came up with the space between the frill and the rounded foot filled with compressed mud, and it seems that the anemone can use this as a more or less solid platform on which to stand. They were problably about 6 inches long when full expanded.

In Liverpool Bay, Nova Scotia, there was a curiously barren beach. The off-lying rocks were densely covered with algae and carried thousands of whelks and sea-urchins, but there was a swell running which made it impossible to land on them. The beach referred to looked like firm brown sand, but was spongy to walk on and turned out to be a peat made of sawdust and chips from a small pulp-mill more than a mile up the bay. This beach was quite extensive, over a foot thick, and seemed to be permanent and it was quite a distinct geographical feature. As the pulp-mill was still small and had been in existence only a few years, it will be interesting to see how this beach develops. It is remarkably barren, containing neither polychaetes, amphipods, nor any other metazoa that I could find.

After leaving New York we went to the Bahamas and spent the next two months in the West Indies, Central America, and the north coast of South America. The weather was ideal for marine collecting, with gentle trade-winds and calms, and good visibility for navigation; no hurricanes came anywhere near us. We made a number of mid-water plankton hauls in deep water, dredged when the bottom was within reach, and at Grand Cayman, Swan Islands, Bay Islands and British Honduras I carried out shallow-water dredging and shore collecting.

The first really interesting catch was a live *Spirula*, which was brought up at Station 15 between Jamaica and Cuba. When the "Challenger" caught its single specimen of *Spirula* in a dredge they naturally thought it was a bottom living animal, but all subsequent evidence goes to show that it lives a planktonic or nektonic life some way below the surface. The "Challenger" specimen may have been caught by the dredge on its way from the bottom to the surface while being hove in. *Spirula* shells occur sometimes in such vast numbers that they form white beaches extending for miles, but until fairly recently the animals themsleves have been very rare in collections. The Cambridge Natural History of 1903 says that there were then only five specimens known, but since then the "Michael Sars" has caught several and the "Dana" about one hundred, so its capture is no longer the event it used to be. Later on we caught three more, all very young. It was interesting to watch the animal alive for some time. Unlike many other cephalopods, such as *Sepia*, it does not lie horizontally in the water but always head down. It swims up and down with its fins, rather slowly, but can also propel itself violently tail first by squirting water from its syphon. (I never saw one eject any ink.) Sometimes it would hang on to the side of the jar for a few seconds, and if one put one's finger in the jar the *Spirula* would at once cling on and nibble gently. In colour the body was white, and curiously rough; this part looked exactly like the ash of a cigar. The tentacles were reddish-brown, the head blue-gray, and the mantle-edge and hinder end reddish brown. Right at the after end between the fins there is a round disc, which the older books describe as a sucker. Schmidt (1922), however, kept *Spirula* alive for some days in the " Dana," and found that this disk is a luminescent organ which gives off a steady but dim light (see also Bruun, 1943). I did not see this myself.

Spirula's habit of swimming constantly with its hind end upper-most may explain why it it is not more often caught. If it is startled by the bridle of the net coming through the water and gives a convulsive leap, it will automatically move several feet straight upwards and the net will pass beneath it. An animal like a prawn such as *Acanthephyra*, which swins horizontally, will shoot off in a horizontal direction when similarly startled and may sometimes go straight into the approaching net.

Just north of Turneffe Island, British Honduras, we used the Agassiz trawl in 500 fathoms. The bottom ranged from fine mud to gravel and was bright yellow in colour. The fauna was rich and included large numbers of *Stephanotrochus diadema*, a deep-sea coral, which is a solitary form like *Fungia*, and is unattached when adult. The tissue is a very deep purplish brown, almost black, and it is disappointing that none of them would expand even in cold water in the dark after being brought on board. *Stephanotrochus* is in some ways a rather unwelcome catch ; near the edge there are twelve very sharp vertical plates standing up a quarter of an inch from the body of the coral, which is itself an inch and a half across ; these plates cut up into ribbons such animals as prawns and polychaetes.

While we were in this region we visited the Bay Islands of Honduras three times. They are high islands, separated from the mainland thirty miles away by water several hundred fathoms deep. The population are mostly English-speaking, as the islands were an informal British colony until a hundred years ago. The most interesting find was enormous quantities of pottery of uncertain age and affiliations which cannot be dealt with here, but in addition to this a gecko turned up in a sackful of lizards which had been bought as food for snakes. According to Parker (1940) this gecko is a new species of *Sphaerodactylus*, a genus which extends all over the Central American and West Indian regions and contains many species, some of which are peculiar to single islands. The Antillean species are distinguished by possessing a groove down the back with very small scales, a feature which is missing in the mainland forms. This Bay Island gecko (*Sphaerodactylus rosaurae* Parker), though so close to the mainland of Honduras, has the groove and small scales, and in this way resembles species living 2,000 miles further east.

We paid three visits to the Bay Islands and two to Swan Islands. The latter are two small coral islands, remarkably interesting to a biologist. They lie about 150 miles off the north-east corner of Honduras, and are surrounded by water of 1,000 fathoms and over ; each island is about a mile and a half long by a mile wide, is composed chiefly of coral limestone, and is densely forested. The western island has a landing-beach and is inhabited by 21 Cayman islanders who grow coco-nuts. They have cattle on the island and rather surprisingly were able to sell us a sheep. This island was used as a careening place by one of the later pirates, Captain Swan, who gave his name to it. There is a large kitchen-midden on the western island containing crude pottery and burnt shells, which shows that Indians once lived there.

The eastern island has no beach and is surrounded by cliffs of 30 to 40 feet, very rough and sharp, which make landing difficult ; it has apparently never been inhabited, even by Indians. It is thickly wooded and has a remarkable fauna, including earthworms, millipedes, centipedes, at least eight species of land gastropods, an iguana, a lizard, a snake, many species of bird, and a mammal peculiar to the island, *Capromys thoracatus*. This is a kind of cavy, about the size of a muskrat but with very coarse fur. It must have as small a range as any mammal ; the other species of the genus are confined to Cuba and Jamaica.

In Stations 28 (off the Bay Islands) and 42 (off N.E. Brazil) we caught in the stramin net 3 and 2 specimens respectively, all young, of the extraordinary deep-sea cephalopod *Vampyroteuthis infernalis*, of which less than a hundred specimens appear to exist. These larvae have been described in detail by Pickford (1939).

Another catch of note was off Grenada in Station 34. Most of the Antilles are very steep-to and surrounded by water too deep for us to dredge in, but three miles off St. George, Grenada, there is a shelf at 450 fathoms on which we towed the Agassiz trawl. It fouled the bottom after 15 minutes, bringing the ship up and bending the trawl frame, but the wire held and the net was undamaged. The bottom appears to be covered with a finely-branching primnoid alcyonarian, *Stenella*, and a singularly beautiful sponge, *Aphrocallistes*. About two bushels of these were in the net, and among them was a remarkable lobster, *Phoberus caecus*, which is one of the largest known deep-sea crustacea. It was pink, with vestigial eyes and very long chelipeds armed with long and very sharp teeth ; the carapace was spiny and rather thin, while the antennae were like wire and over 2 feet in length. As far as I know, only two individuals of this species have been caught before, both by the " Blake " in 1878 on the same grounds ; we were within a mile of the " Blake's " position.

Off the River Orinoco we used the ship's otter trawl three times in order to get some food-fish for the larder. In this we had no luck, but the trawl brought up a number of interesting invertebrates, including the only crinoids caught on the trip and a very fine basket star-fish, *Astrophyton muricatum*. The latter was contracted into a tight ball as big as one's fist but expanded nicely in a bath. It was narcotized successfully with menthol and pickled at its fullest extent. The length of one of the long arms was 47 cm., and the whole animal when extended was more than a yard across.

The rivers of northern British Guiana form an anastomosing series of tidal streams with remarkably turbid water. I collected samples of the water in the Barima and Demerara Rivers, and these have been examined by Dr. L. H. N. Cooper for their light penetration values. These values are so low that it is difficult to understand how any effective photosynthesis can take place in these streams ; nevertheless the animal population is both abundant and varied, including microphagous feeders such as copepods and even bottom-living barnacles, and in the Demerara there were enormous numbers of drifting algae. These water-samples, with some others collected for comparison in the Gambia River, will be discussed by Dr. Cooper and myself in a subsequent paper in this series.

Off northern Brazil we got remarkable catches of pelagic molluscs, including pteropods, heteropods, squids and octopus, and at one station (41) the stramin net distinguished itself by catching a 7-foot blue shark, *Carcharinus* sp. The shark, an immature female, came in dead, but was accompanied by four live remoras. The shark's stomach was quite empty.

To a marine biologist perhaps the most interesting part of the cruise was the crossing of the Central Atlantic from Pernambuco to the Gambia River. Three deep plankton hauls were taken (Stations 43, 45 and 46), in different bodies of water. The two southern stations, in the Equatorial current, were distinguished from all the other midwater hauls in producing neither red *Sagittae* nor red prawns such as *Acanthephyra*. Station 46 was in the east-going Guinea current, where *Acanthephyra* and red *Sagittae* reappeared.

Several remarkable animals were found in these stations. Three squids in particular were unlike any others we caught. One, *Calliteuthis hoylei*, was rufous brown, with markedly retractile and protrusible eyes, and was scattered all over with powerful light organs equipped with lenses ; it must be a brilliant object when illuminated. The other two both had crumpled bag-like bodies, translucent and colourless, and belonged to the group Cranchiidae. Each had two long tentacles dotted with chromatophores, but whereas one had arms of moderate length and very prominent but unstalked eyes, the other had excessively small arms and huge eyes on stalks ; this last has been identified as *Bathothauma lyromma*. Chun (1910, 1915) figures similar forms tightly blown up and consequently streamlined, but our specimens were half deflated while still alive. It is hard to believe that they are very active creatures.

Amphipods were specially numerous in the Central Atlantic, and included several *Phronimae* which actively paddled their cases about for some time after being caught ; but the finest was a perfect specimen of *Cystisoma* about 5 inches in length, colourless except for a yellow stomach and a very faint pink tinge to the legs. It was so transparent that in water the stomach was the only part to be seen, not even the brain and nerves becoming visible until after the animal had been killed and left in formalin for some time. The eyes were enormous, covering the whole dorsal surface of the head, but were colourless and as transparent as the rest of the body. It is hard to understand how these animals can see at all clearly.

An interesting visit was paid to St. Paul's Rocks, which are right in the middle of the Atlantic Ocean, less than a degree north of the Equator. The rocks are only 60 feet high at the most and the most southerly point is less that 300 yards from the most northerly ; probably no part is as much as 10 yards from the sea. This tiny landmass is apparently not of volcanic origin, but is formed of plutonic rocks ; it can with some justice be considered as the world's smallest continent. The rocks stand in 20 or 30 fathoms on a shelf only about half a mile wide, which is surrounded on all sides by water more than 2,000 fathoms deep. As far as we could make out from our echo-sounding gear the sides of the shelf are virtually perpendicular, a feature reminiscent of coral-reefs. No coral, however, is known to occur on St. Paul's Rocks, and they are certainly not a coral-reef. This absence of coral is not easy to understand. When we were there (28.xii.37) the sea-temperature was about 26°C., amply warm enough for reef-building corals, and as the rocks are less than a degree north of the equator it is not be expected that there is a large range of temperature. The rocks are set in the west-going Equatorial Current, which was

STATION LIST

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Station	Date	Position	Depth of sea	Gear	Depth of gear	Remarks
1	27.viii.37	65° 35′ N., 37° 20′ W.	30–50 m.	1. 2-ft. dredge 2. Silk townet	30–50 m. 15–20 m.	Angmagssalik Harbour (E. Greenland).
2	28.viii.37	No catch	—	—	—	—
3	2.ix.37	59° 46′ N., 45° 02′ W.	—	Silk townet	*c.* 15 m.	West Greenland Current.
4	3.ix.37	60° 30′ N., 46° 40′ W.	550 m.	1. 3-ft. dredge	550 m.	Off Julianehaab.
	,,	60° 35′ N., 46° 45′ W.	—	2. Silk townet	*c.* 20 m.	,, ,, (S.W. Greenland).
5	4.ix.37	60° 43′ N., 46° 02′ W.	0–80 m.	1. 2 ft. dredge	*c.* 20 m.	Julianehaab Harbour.
	,,			2. Shore collecting rocks		
	,,			3. Cod long line	80 m.	
6	7.ix.37	60° 06′ N., 45° 25′ W.	110 m.	3-ft. dredge	110 m.	Off Nanortilik (S.W. Greenland).
7	9.ix.37	60° 17′ N., 44° 37′ W.	35 m.	Silk townet	10 m.	Tasermiut Fjord.
	,,	60° 16′ N., 44° 41′ W.	—	Shore collecting	—	,, ,, (S.W. Greenland).
8	11.ix.37	58° 48′ N., 46° 11′ W.	> 2,750 m.	2-m. stramin net	1,300–0 m.	West Greenland Current.
9	22.ix.37	52° 13′ N., 55° 45′ W.	—	Shore collecting	—	N.E. Arm, Horn Bay, Niger Sound, Labrador.
	,,	,,	30 m.	Dip net	Surface	
10	23.ix.37	52° 13′ N., 55° 47′ W.	15 m.	2-ft. dredge	15 m.	N.W. Arm, Horn Bay.
11	26.ix.37	49° 30′ N., 57° 48′ W.	215 m.	Agassiz trawl	215 m.	Bonne Bay, Newfoundland.
12	1.x.37	44° 03′ N., 64° 40′ W.	—	Shore collecting	—	Liverpool Bay, N.S.
13	10.x.37	36° 88′ N., 74° 23′ W.	> 1,800 m.	2-m. stramin net	750–0 m.	Between Gulf Stream and Coast. Probably in counter-current.
14	13.x.37	24° 53′ N., 77° 40′ W.	1,800 m.	2-m. ½-in. meshed townet	900 m.–0 m.	Tongue of the Ocean (Bahamas Is.).

Station	Date	Position	Depth of sea	Gear	Depth of gear	Remarks
	16.x.37	19° 47′ N., 72° 12′ W.	—	Silk townet	Surface	Cap Haitien Harbour (Haiti). (Medusae only.)
15	17.x.37	18° 21′ N., 75° 25′ W.	c. 1,800 m.	2-m. stramin net	c. 1,250 m.–0	Between Cuba and Jamaica.
16	19.x.37	19° 18′ N., 81° 24′ W.	—	Shore collecting	Coral rock,	Georgetown, Grand Cayman.
	,,	19° 18′ N., 81° 22′ W.	2 m.	2-ft. dredge	2 m.	North Sound, ,, ,,
17. A	20.x.37	17° 24′ N., 83° 57′ W.	—	Land collecting	—	Western Swan Island.
B	21.x.37	17° 24′ N., 83° 54′ W.	—	,, ,,	—	Eastern ,, ,,
18	23.x.37	16° 24′ N., 86° 20′ W.	—	Shore collecting	—	George Cay, Port Royal, Roatan Is., Honduras.
19	24.x.37	16° 25′ N., 86° 16′ W.	—	,, ,,	—	Helene Is. Mangroves and coral rock.
20	25.x.37	16° 27′ N., 85° 56′ W.	—	Land collecting	—	Bonacca Is.
21	26.x.37	16° 29′ N., 85° 53′ W.	—	,, ,,	—	Bonacca Is. (All except the Oligochaets labelled Station *20*, but with the correct date, 26.x.37).
	27.x.37	16° 18′ N., 86° 35′ W.	—	Dip net	Surface	Coxen's Hole, Roatan Is.
	28.x.37	17° 28′ N., 88° 11′ W.	—	,,	,,	Belize Harbour, B.H.
22	29.x.37	,, ,,	6 m.	2-ft. dredge	6 m.	,, ,,
23	30.x.37	17° 29′ N., 88° 10′ W.	5 m.	Silk townet	2–3 m.	,, ,,
24	1.xi.37	17° 15′ N., 87° 49′ W.	—	Shore collecting	—	Indian Cay, Turneffe Is.
	,,	17° 16′ N., 87° 50′ W.	4 m.	2-ft. dredge	4 m.	Turneffe Is., B.H.
25	5.xi.37	17° 22′ N., 88° 20′ W.	4 m.	Silk townet	1 m.	North Lake, off Sibun River, B.H. Fresh water.
	,,	,, ,,	,,	2-ft. dredge	4 m.	
26	7.xi.37	17° 53′ N., 87° 44′ W.	c. 900 m.	Agassiz trawl	c. 900 m.	North of Turneffe Is.
27	8.xi.37	16° 22′ N., 86° 40′ W.	—	2-m. stramin net	c. 600 m.–0	Off W. end of Roatan Is.
28	12.xi.37	16° 44′ N., 85° 42′ W.	c. 3,000 m.	,, ,,	c. 1,100 m.–0	N. of Bonacca Is.

STATION LIST—*cont.*

Station	Date	Position	Depth of sea	Gear	Depth of gear	Remarks
29	14.xi.37	17° 19′ N., 83° 57′ W.	1,920 m.	Agassiz trawl	1,920 m.	6 miles S. of Swan Is. Catch, 1 fish.
30	15.xi.37	16° 43′ N., 83° 45′ W.	*c.* 1,000 m.	3-ft. dredge	*c.* 1,000 m.	N. of Bonacca Is. Catch *nil.*
31	16.xi.37	15° 54′ N., 82° 13′ W.	34 m.	,, ,,	34 m.	Off Gorda Cay, Mosquito Bank.
32	17.xi.37	12° 42′ N., 80° 25′ W.	? 2,000 m.	2-m. stramin net	900 m.–0	250 miles N.N.W. of Colon.
	21.xi.37	Cape San Blas, Panama	—	Shore collecting	—	*Littorina scabra.*
33	22.xi.37	11° 00′ N., 75° 43′ W.	*c.* 1,500 m.	2-m. stramin net	*c.* 1,200 m.–0	Off Puerto Colombia.
34	27.xi.37	12° 05′ N., 61° 49′ W.	720–800 m.	Agassiz trawl	720–800 m.	Off St. George, Grenada.
35	1.xii.37	9° 25′ N., 59° 52′ W.	86 m.	Otter trawl	86 m.	Off River Orinoco.
36	2.xii.37	7° 11′ N., 57° 59′ W.	20 m.	,, ,,	20 m.	Off Demerara.
37	6.xii.37	7° 47′ N., 58° 17′ W.	23 m.	,, ,,	23 m.	Off River Essequibo.
	7.xii.37	8° 37′ N., 60° 24′ W.	5 m.	2-ft. dredge	5 m.	Mouth of Barima River, Venezuela. Only dead bivalve shells.
38. A	8.xii.37	8° 15′ N., 59° 45′ W.	—	Silk townet	2 m.	Morowhana, Barima River, B.G. Salinity sample, bottle 139.
B	9.xii.37	,, ,,	12 m.	2-ft. dredge	12 m.	
39	10.xii.37	2 miles S. of St. 38	20 m.	2-m. stramin net	2–3 m.	Junction, Barima and Arouka Rivers, B.G. Salinity sample, bottle 147.
40	13.xii.37	Georgetown, B.G., Demerara River	—	Silk townet	2 m.	Salinity sample, bottle 153.
41	18.xii.37	0° 38′ S., 43° 42′ W.	2,050 m.	2-m. stramin net	900 m.–0	Off N. Brazil. Catch included a 7-foot shark.
42	21.xii.37	5° 51′ S., 34° 38′ W.	2,600 m.	,, ,,	1,200 m.–0	Off N.E. Brazil.

Station	Date	Position	Depth of sea	Gear	Depth of gear	Remarks
43	27.xii.37	3° 35′ S., 32° 20′ W.	2,000 m.	,, ,,	750 m.–0	12 miles N. of Fernando Noronha.
44	28.xii.37	0° 56′ N. c 29° W	50–60 m.	3-ft. dredge	50–60 m.	St. Paul's Rocks shoal.
	,,	,,		Silk townet	2 m.	Close to the Rocks.
45	29.xii.37	4° 15′ N., 26° 20′ W.	c. 4,500 m.	2-m. stramin net	900 m.–0	Northern edge of N. Equatorial Current.
46	30.xii.37	7° 27′ N., 23° 08′ W.	c. 4,400 m.	,, ,,	1,000 m.–0	Guinea Current.
47. A	2.i.38	13° 42′ N., 14° 58′ W.	9 m.	Silk townet	3 m.	Nianimaru, Gambia River. A. Salinity sample, bottle 1.
B	3.i.38	,, ,,	9 m.	2-ft. dredge	9 m.	B. Salinity sample, bottle 17.
48	3.i.38	13° 27′ N., 15° 47′ W.	9 m.	2-m. stramin net	3 m.	Tendeba, Gambia River. Salinity sample, bottle 23.
49	1.ii.38	28° 25′ N., 13° 34′ W.	c. 1,300 m.	Agassiz trawl	c. 1,300 m.	Between Fuerteventura Is. (Canaries) and Africa.

running at about 2 knots on the occasion of our visit. The islands are white with guano, as sooty and noddy terns and boobies all nest there. I believe the only plant life consists of unicellular algae, but a few insects and spiders have been recorded, probably from round the birds' nests which are made of the green alga *Caulerpa.* We were unable to land owing to the surf, but we got some plankton close to the rocks and also dredged in about 40 fathoms from " Rosaura." This was not easy as the bottom is excessively uneven, and also by the time that the dredge has been lowered the ship has nearly drifted off into deep water. All we got was a sponge with numerous epiphytes and commensal animals, and several fragments of algae, notably of *Caulerpa* and *Halimeda*, genera which are both characteristic of warm seas and especially of coral-reefs.

Our last haul was made with the Agassiz trawl in more than 700 fathoms between the Canaries and the African mainland. Our position coincided with that of Station 41 in the 1910 cruise of the " Michael Sars " (Murray & Hjort, 1912), and the two catches appear to have been very similar. We brought up many fish such as the macrurid *Coelorhynchus labiatus*, and a large number of eels, *Synaphobranchus pinnatus*, which were very much alive when they came up, about a score of them swimming out of the net when it reached the surface ; this was after they had been raised from a depth of 700 fathoms or so in just over half an hour. The catch included many abyssal crustacea, and also a number of soft flexible sea-urchins of the species *Sperosoma grimaldii* and *Calveriosoma hystrix.*

The whole collection from the cruise was deposited in the British Museum (Natural History).

I owe a great debt of gratitude to the late Lord Moyne for taking me on this cruise and for making these collections possible. I would also like to express my sincere thanks for the friendly co-operation of the late Captain H. M. S. Laidlaw, R.N.R., and the officers and crew of the " Rosaura," to whose collective skill the successful completion of these hauls was due.

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2. UNDER-WATER ILLUMINATION AND ECOLOGY IN TROPICAL ESTUARIES

By JOHN S. COLMAN AND L. H. N. COOPER

LITTLE accurate information is available on the penetration of daylight in the estuaries of tropical rivers. During the cruise of M.Y. " Rosaura " in the winter of 1937–38, surface water samples were collected and brought back to Great Britain for salinity analyses by the Government Chemist. These in some cases proved a matter of difficulty owing to the excessive colour of the water. Since this colour appeared likely to have considerable ecological importance, the Government Chemist kindly returned the water samples to the Plymouth Laboratory where extinction coefficients were determined in the Pulfrich Photometer with nine spectral filters as described by Cooper & Milne (1938, 1939). The extinction coefficient, μ, is defined by the equation

$$\mu d = 2{\cdot}303 \log_{10} \frac{I_0}{I_1},$$

where d is the length of the column of water measured in metres and I_0 and I_1 are the intensities of light of a given wave-length entering and leaving the water sample. Three months elapsed between collection and the light measurements on 22nd March, 1938, so that there was time for bacterial action considerably to affect the colouring matter. Admixture of salt water may lead to " clumping " or coagulation of colloidal matter.[1] The results are sufficient to show that exceptional opacity existed in the Barima river and in the Demerara river at Georgetown, both in British Guiana (Tables I and II). Blue and green light were even more heavily absorbed than were red and yellow. Data for Neal Point, the most turbid station investigated in the Hamoaze (Tamar Estuary) near Plymouth, England, are included for comparison. If the zone of active photosynthesis be considered as lying

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[1] In 1945 extinction coefficients of sea water determined by one of us with the Pulfrich photometer were compared with coefficients determined on " brightness profiles " by an aerial photographic method (Moore, 1947, Table 8). In some cases determinations in the photometer were twice as great. Since no firm explanation was apparent publication has been deferred. Poole & Atkins (unpublished work) have since found a similar discrepancy between extinction coefficients determined with the Pulfrich photometer and those measured in the sea with submarine photometers. It has become clear that the extinction coefficient, measured on a beam of light passing through water enclosed in a tube in a Pulfrich photometer, or probably in any similar visual or photoelectric laboratory absorptiometer, is a very different physical quantity from the vertical extinction coefficient measured by a submarine photometer exposed in the sea or the extinction coefficient determined photographically from brightness profiles. Poole & Atkins explain the discrepancies as due to the forward scattering which they find light to undergo in natural waters. Results with the Pulfrich photometer or any other laboratory absorptiometer employing a beam of light in a tube have value, but they are not the same as those obtained by direct observation at sea or from the air. (Added in proof, 23.ix.53.) There is yet another factor, in addition to the effect of forward scattering from natural waters confined in glass tubes, which Cooper now accepts without reserve. It has been found, following a suggestion of Dr. H. H. Poole, that the geometry of the Pulfrich measuring assembly, as we have used it, makes for an apparent extinction coefficient larger than that obtained by other methods. Comparison with results obtained by Cooper and Milne with the same apparatus is legitimate. Comparison with any other procedure may not be.

TABLE I.—*Hydrographical Data*

Station No.	Name	Date	Position	Depth of river (m.)	State of tide	Surface Salinity (‰)	Surface Temperature (° C.)
38B	Morowhana, Barima River, British Guiana	9.xii.37	8° 15′ N., 59° 45′ W.	12–20	Ebb	10·90	..
39	Junction of Barima & Arouka Rivers, British Guiana	10.xii.37	2 miles above (south of) Station 38B	20	,,	8·3*	26°
40	Demerara River, Georgetown, British Guiana	13.xii.37	..	7	Flood	13·9*	..
47A	Nianimaru, Gambia River	2.i.38	13° 42′ N., 14° 58′ W.; 120 miles from mouth	9	Ebb	0·00	24°
47B	Nianimaru, Gambia River	3.i.38	13° 42′ N., 14° 58′ W.; 120 miles from mouth	9	..	0·00	..
48	Tendeba, Gambia River	3.i.38	13° 27′ N., 15° 47′ W.; 50 miles from mouth	9	1 hr. after high water	2·63	24°

* Salinity is only approximate owing to uncertainty of end-point.

TABLE II

Station No.	Spectral filter number / Centre of gravity of filter (mμ.)	S43	S47	S50	S53	S57	S61	S66·6	S72	S75
		434	463	494	530	572	619	666	729	750
Extinction Coefficients, μ_{DW} as measured with nine spectral filters:										
38B	Morowhana, Barima River	30·7	24·4	19·7	15·6	13·1	10·9	9·4	9·2	10·0
39	Junction of Barima and Arouka Rivers	39·9	30·3	24·8	20·1	16·9	14·3	12·0	11·9	11·1
40	Demerara River, Georgetown	27·2	24·6	23·1	21·4	19·5	19·3	18·5	18·8	23·9
47B	Nianimaru, Gambia River	6·5	5·9	5·25	4·85	4·80	4·45	4·20	5·35	6·1
	Neal Point Buoy, River Tamar, England, low water springs 16.ii.37	18·8	16·5	15·0	14·6	13·4	12·8	—	13·5	12·7
	Ditto, 23.vi.37	6·18	5·48	5·01	4·62	4·63	4·53	—	5·61	6·29
	Neal Point Buoy, River Tamar, England, high water neaps, 17.vi.37	2·11	1·87	1·71	1·58	1·60	1·79	—	3·18	3·86
Depths in metres at which intensity of light is reduced to 1% of that incident on surface (no correction for surface loss):										
38B	Morowhana, Barima River	0·15	0·19	0·23	0·29	0·35	0·42	0·49	0·50	0·46
39	Junction of Barima and Arouka Rivers	0·12	0·15	0·19	0·23	0·27	0·32	0·39	0·39	0·42
40	Demerara River, Georgetown	0·17	0·19	0·20	0·22	0·24	0·24	0·25	0·24	0·19
47B	Nianimaru, Gambia River	0·71	0·78	0·88	0·95	0·96	1·04	1·10	0·86	0·76
	Neal Point Buoy, River Tamar, England, 16.ii.37	0·24	0·27	0·30	0·30	0·33	0·35	—	0·33	0·35
	Ditto, 23.vi.37	0·72	0·81	0·89	0·96	0·96	0·98	—	0·79	0·71
	,, 17.vi.37	2·10	2·38	2·60	2·81	2·77	2·48	—	1·39	1·15

mainly above the level of 1% illumination (Table III) it must be confined to a layer no more than 40 cm. thick.

Cooper & Milne (1939) found a close relation between the daylight factor and zonation of algae on buoys moored in Plymouth Sound and the Hamoaze. The daylight factors at the boundaries between the algal Zones I and II and between Zones II and III lay at about 80% and 60% respectively. The depths in the tropical estuaries corresponding to these daylight factors are set out in Table IV in which the corresponding Plymouth data are given for comparison. The same distribution of algae is not to be expected in such widely different environments, but even so the daylight factor shows very clearly how greatly the zone of active photosynthetis must be compressed.

The maximum intensity of tropical sunlight is only about 30% greater than that of the brightest summer day in Southern England, but there are two periods with zenithal sunlight each year and the average solar altitude is considerably greater (Atkins, Ball and Poole, 1937). Even so a dearth of phytoplankton and of the animals dependent thereupon might be expected. A comparison with the conditions actually found is thus of interest.

A. BRITISH GUIANA

Station 38 : Morowhana, Barima River, 8–9.xii.37

The river is tidal, about 300 metres wide and from 12 to 20 metres deep, and the salinity on the ebb was 10·90‰. The water is apparently sometimes fresher than this, for the local inhabitants are said to drink it. A haul with the 2-foot dredge brought up mud and rotting vegetation, and nothing living except some barnacles (young *Balanus* sp. in the Tetraclita stage) on a stone. The zooplankton, sampled with a silk townet (56 meshes to the linear inch), was quite abundant and included the following forms :[1]

Pisces :	Engraulidae :	Larvae under 20 mm.	15
	Sciaenidae :	,, ,, ,,	22
	Gobiidae :	,, ,, ,,	1
	Chaetodipteridae :	*Chaetodipterus faber* (Brouss.) 14 mm.	1
	Tetrodontidae :	*Colomesus psittacus* (Schn.) 15 mm.	2
Mollusca :	Gastropoda, young,		Several
Crustacea :	Decapoda :	Sergestidae,	,,
		Penaeus sp., young	Many
		Zoeas,	,,
		Other larvae,	,,
	Amphipoda :	in tubes,	Several
	Isopoda :		2
	Copepoda :	including *Labidocera fluviatilis* Dahl *Acartia lilljeborgi* Giesbr. *Acartia giesbrechti* Dahl.	Many
Chaetognatha :	*Sagitta* sp., small		Many
Coelenterata :	Scyphomedusae :	*Stomolophus meleagris*, young,	3

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[1] Such numbers of animals as are given in this paper must be regarded only as indications of relative abundance.

The bulk of the catch consisted of zoeas, copepods and *Sagittae*. The presence of the first two of these groups suggests that some planktonic plant-food must have been present in spite of the low level of under-water illumination.

Station 39 : At the junction of the Barima and Arouka Rivers, 2 miles above Station 38, 10.xii.37

The salinity on the ebb was 8·3‰. The river was remarkably full of fish, many of which must have weighed several pounds. The plankton was here sampled with a 2-m. stramin net (about 16 meshes to the linear inch), streamed from the ship while at anchor. The catch was large but contained no zoeas, copepods or *Sagittae* ; these would all have passed through the meshes of the net. The following forms were caught :

Pisces :	Engraulidae :		>80
	Ariidae :	*Tachysurus nuchalis* (Gunther,) 30 mm.	1
	Sciaenidae :	*Stellifer stellifer* (Bloch), 10–35 mm.	15
	Gobiidae :	post-larval, 27 mm.	1
	Soleidae :	*Achirus* sp., 23 mm.	1
	Cynoglossidae :	*Symphurus* sp., 33 mm.	1
	Mugilidae :	*Mugil* sp., 40 mm.	1
	Tetrodontidae :	*Colomesus psittacus* (Schn.), 20 mm.	>100
	Also several larval fish, unidentified.		
Crustacea :	Decapoda :	*Xiphopenaeus kroyeri* (Heller), small	2
		Penaeus sp., very small	Many
		Sergestidae, young	2
		Palaemon sp.	Several
		Prawns, not determinable	,,
	Amphipoda :	*Pseudoceradocus lutzi* Schoemaker	1
		Isopoda :	5
Coelenterata :	Scyphomedusae :	*Stomolophus meleagris*, adults	5

Station 40 : Demerara River at Georgetown, B.G., 13.xii.37

The river is here about a mile wide and the ship lay only one mile from the open, though very shallow, sea. (There is a depth of only about 8 metres 15 kilometres off shore). The tide ebbs and flows at about 5–6 knots, and on the ebb the salinity was 13·9‰. The water was so turbid that if one's hand was immersed to the wrist the fingers were invisible. The tidal current in 7 metres of water no doubt keeps the water well stirred right down to the bottom. This is suggested also if we compare the extinction coefficients in the Demerara river with those in the neighbouring Barima. Whereas the Barima is strongly coloured brown and shows much the greater absorption in the blue and violet, the Demerara shows a more uniform absorption through the spectrum, suggesting that a non-selective absorption due to suspended detritus is super-imposed on selective absorption due to brown pigments in true or colloidal solution in the water. (The tidal current in the Barima is less than half that in the Demerara.) The very rapid extinction of under-water illumination must confine active photosynthesis to a very shallow layer. Jenkin (1937) found that the compensation point for *Coscinodiscus excentricus* lay at about 360 lux. This is a mean figure for 24 hours. For the hours of daylight it would be considerably higher. If we take 140 kilolux as a round figure for midday tropical daylight (Atkins, Ball & Poole, 1937) the daylight factor for *Coscinodiscus* would exceed $\frac{0\cdot36}{140} = 0\cdot26\%$. The value 1% for the daylight factor over 24 hours is therefore about as near as we can get at present. Reflection losses at the surface may also reduce the incident light by 4 to 15% according to the degree of roughness. Moreover land plants, and no doubt marine algal also, differ greatly in their response to light. Even so, under the most favourable conditions the depth of the layer of active photosynthesis could not have exceeded one-third of a metre, but nevertheless, the river was full of algae in globular masses up to about an inch in diameter and occurring every few inches; they were covered with brown detritus but appeared to be healthy, and were certainly not confined to the surface.

The plankton was sampled with the silk net, which soon became completely clogged with these algae so that the catch was small, though it was probably fairly representative qualitatively. It contained:

Pisces:	Engraulidae		2
	Unidentified		1
Crustacea:	Decapoda:	*Penaeus* sp., young	A few
	Cumacea		2
	Amphipoda:	small	1
	Copepoda:	including *Acartia lilljeborgi* Giesbr.	Many
Chaetognatha:	*Sagitta* sp., small		,,
Coelenterata:	Scyphomedusae:	*Stomolophus meleagris*, young	3
	Ctenophora		1

Here again the presence of copepods seems to indicate unicellular plants on which they feed, this in spite of the great opacity of the water. The two cumaceans must represent a bottom fauna living in perpetual darkness. The occurrence of a ctenophore in water with a salinity as low as 13·9‰ is perhaps worth noting.

The abundance of living organisms in these Guiana estuaries is much greater than would be anticipated from the conditions of illumination, and a quantitative ecological study should prove of considerable interest. Many marine animals grow to a large size in the ocean abyss far below the region of active photosynthesis. They depend on the rain of food from the illuminated waters above. Similarly many of the animals described above from tropical rivers must have sought their food in the vegetable and animal detritus brought down from the rain forest and from more transparent inland waters.

B. GAMBIA RIVER, WEST AFRICA

Station 47: Nianimaru, 2.i.38

Nianimaru, where the river is nearly a kilometre wide, lies about 200 km. from the mouth of the Gambia river, which remains tidal for yet another 210 km. Even so the surface water was perfectly fresh, with a salinity of 0·00‰ just after high-water. The plankton, sampled with the silk net on the ebb, was of a fresh-water type, containing many reproducing cladocera, *Bosmina coregoni*, but nothing else. The 2-foot dredge, shot in 9 metres, came up full of mud devoid of anything living. The spectral absorption of the water was uniform and in no way remarkable. The depth of 1% illumination lay at 94 cm. so that the conditions for photosynthesis were much more favourable than in the Guiana rivers investigated, where the corresponding depths ranged from 22 to 40 cm. (see Table III).

TABLE III.—*Depth in metres at which total visible radiation was reduced to 1% of that incident on the surface. No correction for surface loss*

Station No.	Place	Depth m.
38B	Morowhana, Barima River	0·40
39	Jct. of Barima and Arouka Rivers	0·31
40	Demerara River, Georgetown	0·22
47B	Nianimaru, Gambia River	0·94
	Neal Point Buoy	0·3–2·2*

* The lower figure applies only for short periods near low water during wet weather in winter. For much of the year at this turbid station the depth of 1% illumination is likely to exceed 1·5 m.

TABLE IV.—*Depth in metres at which daylight factors of* 80% *and* 60% *would be found* (*corresponding to the zonal boundaries of Cooper & Milne* (1939, *revision of Table V, p.* 395)

Zonal boundary	I–II	II–III
Daylight factor	80%	60%
Guiana rivers:		
Morowhana, Barima R.	0·0155	0·035
Jct. of Barima and Arouka	0·011	0·027
Demerara, Georgetown	0·010	0·024
Gambia River, Nianimaru	0·040	0·100
English estuary:		
Plymouth Sound	0·180	0·356
Hamoaze Buoys Nos. 4, 7 & 11	0·08–0·10	0·18–0·25

Station 48: Tendeba, 3.i.38.

Tendeba is some 120 km. below Nianimaru and about 80 km. from the mouth of the river. The surface salinity was 2·63‰ one hour after high-water. The plankton was sampled with the stramin net and appeared to be not markedly more numerous than and definitely not so varied as in the much darker waters of the Barima river. The catch contained:

Pisces:	Clupeidae:	*Pellonula afzeliusi* Johnels	>200
	,,	*Ilisha africana* (Bloch) 115–130 mm.	2
	Sciaenidae:	*Johnius elongatus* (Bowdich) 58–65 mm.	2
	Atherinidae:	Larvae, <15 mm.	>25
Crustacea:	Decapoda:	*Callinectes latimanus* Rathbun,[1] female	1
		Penaeus sp., immature	Many
		Crangonidae, immature	,,
	Mysidacea		Abundant
	Isopoda		1
Nematoda			1

[1] Several other crabs, presumably of this species and up to 10 cm. across, were seen at the surface drifting with the tide.

No copepods or *Sagittae* were caught, but they may have passed through the meshes of the net. The plankton at this station was remarkably colourless.

We are indebted for the names of species to the following specialists: Dr. I. Gordon (Decapods and Amphipods), Dr. J. Harding (Copepods), Lieut.-Col. W. P. C. Tenison, D.S.O., and Mr. D. W. Tucker, (Fish) and Capt. A. K. Totton (Coelenterates); also to Dr. W. R. G. Atkins, F. R. S., for discussion of the conditions of illumination and photosynthesis.

SUMMARY

Waters from the tidal estuaries of the Rivers Barima and Demerara in British Guiana show extremely heavy absorption of light of all wave-lengths; nevertheless, in spite of the unfavourable conditions for photosynthesis, the zooplankton is both varied and abundant. These observations in rivers of British Guiana are compared with similar ones made in the Gambia River, West Africa.

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3. THE ECHINODERMATA

By D. DILWYN JOHN AND AILSA M. CLARK

With Plate 6 and Text-figs. 1–12.

THE collection of Echinoderms taken by the "Rosaura" includes specimens from off Greenland and north-east America, as well as from the West Indies and one station off the north-west coast of Africa.

Some of the Echinoids were identified by the late Dr. Th. Mortensen before the war. The work was continued by one of us (D. D. J.), who described those species which are new and commented on various other species; the remarks about the new species and the remaining specimens, the preparation of the figures and the final compilation were done by the other (A. M. C.).

The species taken are as follows (those marked with an asterisk being mentioned in the text):

Name	Station	Number of specimens
Asteroidea		
Ctenodiscus crispatus (Retzius) . .	11 (Newfoundland) and 6 (S.W. Greenland)	54
Astropecten marginatus Gray . .	36 (British Guiana)	3
Astropecten antillensis Lütken . .	35 (off R. Orinoco)	2
Astropecten articulatus (Say) . .	35 ,, ,, ...	1
**Tethyaster vestitus* (Say) . . .	35 ,, ,, ...	1
****Luidia rosaurae*** sp. n.	35 ,, ,, ...	3
****Luidia barimae*** sp. n.	35 ,, ,, ...	2
Luidia senegalensis (Lamarck) . .	36 (British Guiana)	1
Luidia clathrata (Say)	22 (British Honduras) and 37 (Brit. Guiana)	2
Anthenoides piercei Perrier . .	35 (off R. Orinoco) and 36 (Brit. Guiana)	4
Nymphaster arenatus (Perrier) . .	26 (Brit. Honduras) and 49 (off N.W. Africa)	3
Goniaster cuspidatus Gray . . .	26 (Brit. Honduras) and 35 (off R. Orinoco)	2
**Ceramaster granularis* forma *balteatus* (Sladen)	49 (off N.W. Africa)	9
Echinaster sentus (Say)	35 (off R. Orinoco)	1
Henricia sanguinolenta (O. F. Müller) .	10 (South Labrador)	1
Crossaster papposus (Linnaeus) . .	10 ,, ,, and 11 (Newfoundland)	2
**Brisingella coronata* (G. O. Sars) . .	49 (off N.W. Africa)	1
*Brisingidae—fragment	26 (British Honduras)	1 arm
Zoroaster ackleyi Perrier	26 ,, ,, ...	1
**Stephanasterias albula* (Stimpson) .	6 (S.W. Greenland)	2
Leptasterias polaris (Müller & Troschel)	9 (South Labrador)	1

Name	Station	Number of specimens
Ophiuroidea		
Astrophyton muricatum (Lamarck)	35 (off R. Orinoco)	1
Astroporpa annulata Lütken	35 ,, ,,	4
Ophiacantha pentacrinus Lütken	34 (Grenada)	1
Ophiacantha metallacta H. L. Clark	34 ,,	116
Ophiacantha bidentata (Retzius)	11 (Newfoundland)	2
Ophiomitra valida Lyman	34 (Grenada)	3
* **Ophioplinthaca grenadensis** sp. n.	34 ,,	1
Ophioplinthaca incisa (Lyman)	34 ,, and 26 (Brit. Honduras)	5
Amphiura sundevalli (M. & Tr.)	1 (Greenland)	1
* *Amphipholis gracillima* (Stimpson)	22 (British Honduras)	6
Ophiactis savignyi (M. & Tr.)	31 (Mosquito Bank, W.I.)	1
* *Ophiactis abyssicola* (Sars)	49 (off N.W. Africa)	10
Ophiopholis aculeata (Linnaeus)	1, 4, 6 (Greenland) and 10 (S. Labrador)	c. 34
* **Ophionereis dolabriformis** sp. n.	35 (off R. Orinoco)	1
Ophiocoma echinata (Lamarck)	16 (Grand Cayman Id.)	2
Ophioderma brevicaudum Lütken	37 (British Guiana)	2
* *Amphiophiura metabula* H. L. Clark	34 (Grenada) and 26 (Brit. Honduras)	6
Ophiocten sericeum (Forbes)	1 (Greenland)	6
Stegophiura nodosa (Lütken)	10 (S. Labrador)	1
* *Ophiomusium validum* Ljungman	26 (British Honduras)	65
Ophiolepis elegans Lütken	31 (Mosquito Bank, W.I.)	3
Ophiura sarsi Lütken	6 (Greenland) and 11 (Newfoundland)	45
* *Ophiernus adspersum* Lyman	34 (Grenada) and 26 (British Honduras)	6
Echinoidea		
Tretocidaris bartletti (A. Agassiz)	35 (off R. Orinoco)	5
Salenocidaris rarispina A. Ag.	26 (Brit. Honduras) and 49 (off N.W. Africa)	7
Plesiodiadema antillarum (A. Ag.)	26 (Brit. Honduras) and 49 (off N.W. Africa)	2
Sperosoma grimaldii Koehler	49 (off N.W. Africa)	9
Calveriosoma hystrix (W. Thomson)	49 ,, ,,	4
Phormosoma placenta W. Thomson)	49 ,, ,,	1
Tripneustes ventricosus (Lamarck)	18 (Honduras)	2
Strongylocentrotus dröbachiensis (O. F. Müller)	1, 5 (Greenland), 9, 10 (South Labrador) and 12 (Nova Scotia)	c. 30
Holothuroidea		
Holothuria mexicana Ludwig	16 (Grand Cayman Id.)	1
Mesothuria gargantua Deichmann	26 (British Honduras)	1
Phyllophorus pellucidus (Fleming)	6 (Greenland)	1
Chiridota laevis (Fabricius)	5 and 6 (Greenland)	12
Crinoidea		
Tropiometra carinata (Lamarck)	37 (British Guiana)	10

Class ASTEROIDEA

Family ASTROPECTINIDAE

Tethyaster vestitus (Say)

Asterias vestita Say, 1825 : 143.
Sideriaster ? vestitus, Verrill, 1915 : 193.

St. 35. 9° 25′ N., 59° 52′ W. (off the mouth of the river Orinoco) ; otter trawl ; 86 m. One specimen.

$R = 70$ mm., $r = 16$ mm. $R/r = 4{\cdot}3/1$.

This name was eventually arrived at after a great deal of correspondence with Mr. Austin Clark of Washington. He has recently received a huge Astropectinid from off North Carolina which answers very well to Say's description of *Asterias vestita* as far as that goes. This specimen has $R = 250$ mm., with a diameter of about 18 inches, probably as, compared with one of 14 inches for Say's lost type from Cape May, New Jersey, and it almost certainly represents the same species. A notable feature of this form is the development of large spatular ventro-lateral and infero-marginal spines, similar to, but less well-developed than, those of *Archaster magnificus* Bell from St. Helena in the south-east Atlantic. One of Bell's types with $R = 215$ mm., has these spines so large as to overlap, producing a very "shaggy" appearance, each spine being about 6 mm. long, whereas in the even larger specimen from North Carolina these spines are only about 4 mm. long. There seems to be no other significant difference between the two forms. Caso (1947 : 225) appears to think that *magnificus* is synonymous with *Sideriaster grandis* Verrill from the Gulf of Mexico. This opinion was shared by Mr. Clark and Dr. W. K. Fisher, but on the evidence of a number of specimens from the type locality Mr. Clark now concludes that *grandis* also is distinct from both *magnificus* and *vestitus*, being differentiated by the pointed (rather than truncated) form of the ventro-lateral and infero-marginal spines, developed only at a late stage (when R is more than 150 mm.) as in the latter. This is coupled with other features such as the relatively shorter dorsal paxillae in *grandis*.

The specimen taken by the " Rosaura " is too young for the ventro-lateral spines to have developed, so that it is not absolutely certain whether it represents *vestitus* or *grandis*. However, Mr. Clark has a large specimen with $R = 160$ mm. from Porto Rico which has small blunt ventro-lateral spines like *vestitus*. He therefore believes that *vestitus* occurs in the West Indies as well as up the East coast of the United States as far as New Jersey while *grandis* is limited to the Gulf of Mexico. This is similar to the distribution of *Astropecten articulatus* (Say), which extends from North Carolina (? New Jersey) south to Uruguay with a subspecies *valenciennі* in the Gulf of Mexico, as pointed out by Mr. Clark. Whether the two forms of *Tethyaster* are specifically or subspecifically distinct is controversial.

As for the generic name used here, it was finally decided that *Tethyaster* Sladen with genotype *Asterias subinermis* Philippi embraces all the species formerly included in *Sideriaster* Verrill and *Moiraster* Sladen as well as *Anthosticte* Fisher. This amalgamation will be discussed in more detail in a separate paper on *Tethyaster* by A. H. Clark and A. M. Clark. It is sufficient here to list the species included in the genus.

subinermis (Philippi) (genotype) .	Mediterranean, Bay of Biscay to Mauritania.
vestitus (Say)	New Jersey to Venezuela.
grandis (Verrill)	St. Helena and Ascension.
magnifica (Bell)	Gulf of Mexico.
aulophora (Fisher) . . .	Philippines.
canaliculatus (A. H. Clark) . .	Gulf of California.
gigas (Caso) (possibly only the large form of *canaliculatus*)	Gulf of California.
pacei (Mortensen) . . .	South Africa.

Family Luidiidae

Luidia rosaurae sp. n.

(Pl. 6 fig. 1 ; Text-figs. 1 and 2)

St. 35. 9° 25′ N., 59° 52′ W. (off the mouth of the river Orinoco) ; otter trawl ; 86 m. Three specimens.

Diagnosis. A species of *Luidia* with five rays belonging to the *Alternata* group of Döderlein ; no enlarged dorsal spines present ; the paxillae of the two outermost rows larger than those of the supero-marginal series ; pedicellariae present on many of the dorsal paxillae particularly the lateral ones, as well as on the infero-marginal plates ; four adambulacral spines on each plate, the two outermost arranged in a line parallel to the furrow ; three- or four-valved pedicellariae on the ventro-lateral plates of many segments, especially proximally ; one large marginal spine on each infero-marginal plate with small appressed ones on the ventral surface of the plate.

Description. The three specimens are all rather broken. Each has five rays. In the only one which has a complete and original (i.e., not regenerated) arm, R is about 53 mm. and r is 6·5 mm. $R/r = 8/1$.

The three outer rows of paxillae on the arms are larger than the remainder ; the paxillae of the second and third rows are larger than those of the first. The paxillae of the first (i.e., supero-marginal) series, are rectangular, being slightly elongated. Those in the proximal part of the arm consist of 25–30 spinules, five to eight of which are in the centre, the remainder around the edge. In the centre of most there is also a small bivalved pedicellaria. The paxillae of the second and third rows are rectangular, being slightly longer in a transverse than a longitudinal direction ; those shown in fig. 2 are foreshortened. At the base of the arm they consist of about 30 to 38 spinules, of which 14 to 16 are in the centre. The central spinules are heavier and blunter than the peripheral ones. A small number of these paxillae have two-valved pedicellariae among the central spinules.

The paxillae occupying the centre of the arm are smaller and roughly circular. At the base of the arm there are eight or nine rows of them, of which those of the outer row on either side are slightly larger than the remainder. They consist of a central group of 14 to 16 spinules, of which those nearest the centre are heavy and blunt, and a peripheral circle of about the same number of spinules. In the paxillae in the middle of the arms the contrast between the central and peripheral spinules is more marked. There are up to eight central spinules, of which some or all are considerably heavier than the peripheral ones, of which there are about ten. These paxillae are very variable. They do not form regular rows. Those at the centre of the disc are of the same nature but smaller and more crowded.

The innermost adambulacral spine arises within the furrow. It is long and compressed and strongly recurved. A second and similar spine, not quite so recurved, occurs just outside it. External to this are two slightly shorter spines standing side by side; they are straight and compressed and taper from a wide base to a narrow tip. The outer part of the adambulacral plate is partly overlapped by the ventrolateral plate which frequently carries a large and conspicuous three-or four-valved pedicellaria as well as several spinules. The pedicellariae are most numerous near the interbrachial angles.

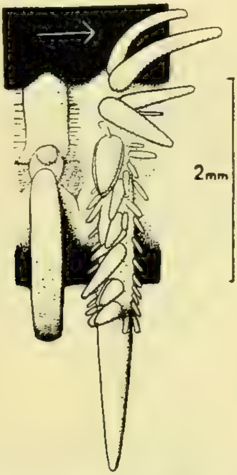

FIG. 1. *Luidia rosaurae* sp. n. Type. Ventral view of one side of two adjacent joints, that on the left having been denuded with sodium hypochlorite. (The spines are displaced sideways to avoid foreshortening as much as possible; the arrow points towards the mouth.)

The underside of each infero-marginal plate is raised into a strong ridge, the adjacent ridges being separated by deep grooves. The outer surfaces of the ridges are occupied by flattened spinelets of medium but varying lengths; fine spinules arise from the edges of the ridges. Near the outer edge there are often one or two pedicellariae, smaller than those of the ventro-lateral plates, of two, or more rarely three, valves. One strong, somewhat flattened, tapering spine nearly 2 mm. long arises from near the upper edge of each plate forming a regular border to the arm. There is a paxilla-like group of spinules with one or two bi-valved pedicellariae above each spine, at least at the base of the arm. The outer parts of the arms are rather badly damaged.

When freshly preserved one of the specimens was straw coloured, with a brown patch in the centre of the disc continuous with broad brown bars running a short distance down the middle of each arm; there were also brown bands across the outer parts of the arms at intervals. The other two specimens were brown, but with deeper colour in areas corresponding to the brown parts of the first specimen. (After 15 years all colour has been lost.)

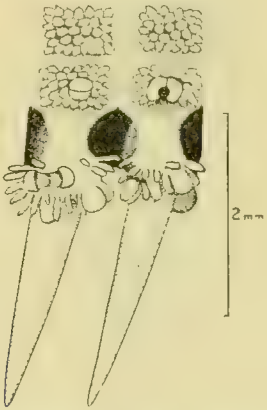

FIG. 2. Dorsal view of the top of two infero-marginal plates (seen in profile because of distortion in preservation causing an abrupt bend just above these plates) and the adjacent paxillae.

REMARKS. This species is obviously most closely related to *Luidia scotti* Bell (1917 : 8), which is described fully in the third note on Asteroids in the British Museum by A. M. Clark (1953 : 383). The types of *L. scotti* were taken off Rio de Janiero in 40 fathoms (73 metres). They differ from *L. rosaurae* chiefly in having much thicker, more stumpy spines and spinules on the ventral plates, a second enlarged marginal spine above the ambital one on the infero-marginals, and in having fewer ventro-lateral and infero-marginal pedicellariae and no dorsal ones.

This last character—the abundance of pedicellariae—is probably not of sufficient value to be used alone for specific distinction but the three points taken together are enough, on the evidence of the material available, to distinguish the two forms as separate species.

The second point is interesting since in the types of *Luidia doello-juradoi* Bernasconi (a synonym of *L. scotti* in the opinion of A.M.C.) from off Buenos Aires (Bernasconi, 1941 and 1943) the two large marginal spines on each infero-marginal plate are said to be nearly the same size, the upper being only slightly smaller. In the types of *L. scotti* the upper spine averages only one-third of the length of the lower one, although occasionally it is two-thirds as long.

Luidia armata Ludwig (1905 : 85) from the Gulf of Panama also has much in common with *Luidia rosaurae* but perhaps even more with *L. scotti*. It has ventro-lateral pedicellariae only in the interbrachial angles, but also has dorsal pedicellariae on the supero-marginal paxillae. Figures of this and of the other related species of *Luidia* described from Central and South America will probably show that they cannot all be maintained as valid species. This may be true of *Luidia armata* Ludwig, *L. ludwigi* Fisher (1906 : 122 and 1911 : 113), *L. scotti* Bell, *L. doello-juradoi* Bernasconi and *L. rosaurae*, which could represent local forms of a single species occurring on both sides of South and Central America. However, without Pacific specimens for comparison this suspicion cannot be verified.

Luidia barbadensis Perrier (1881 : 29) also appears to be related to *L. rosaurae*. It is apparently usually six-rayed, whereas the three specimens of *L. rosaurae* are all five-rayed. The only pedicellariae described in *L. barbadensis* are said to be on the adambulacral plates (probably these are actually on the ventro-lateral plates as in related species) and in the interradial areas (Verrill, 1915 : 205–7). In *Luidia rosaurae* they also occur on the outer paxillae of the arms dorsally and on the outer and lower surfaces of the infero-marginal plates. The infero-marginal plates of *L. barbadensis* bear *two* large spines on the margin of the ray. In *L. rosaurae* there is only one large marginal spine. There are also differences in the arrangement and proportions of the adambulacral spines of the two species. In the type of *L. barbadensis* with R = 125 mm. there are only two spines behind the furrow spine not three as in *L. rosaurae*, although Verrill (1915 : 207) describes an " Albatross " specimen of *L. barbadensis* with four adambulacral spines arranged as in this new species.

A good series of specimens of *Luidia barbadensis* or detailed figures of the types are needed to define more clearly the relationships of the species.

Perrier's other six-rayed species *Luidia convexiuscula* (1881 : 30), is based on a specimen with R only 28 mm. There appears to be no significant difference by which it can be distinguished from *L. barbadensis*, taking into account the very considerable size discrepancy between the types of the two species. The presence of three-valved pedicellariae only in the arm angles, only one enlarged marginal spine and the poor development of the adambulacral spines would be expected in such a young specimen.

Luidia barimae sp. n.

(Pl. 6, fig. 2 ; Text-figs. 3 and 4)

St. 35. 9° 25′ N., 59° 52′ W. (off the river Orinoco) ; otter trawl ; 86 m. Two specimens.

DIAGNOSIS. A ten-rayed species of *Luidia* belonging to the *Quinaria* group of Döderlein, with all the dorsal paxillae irregularly arranged, some of them with one or more pedicellariae ; no spino-paxillae ; three adambulacral spines in a row at right angles to the furrow ; one to four ventro-lateral pedicellariae ; no furrow pedicellariae except on the mouth plates ; infero-marginal plates extending on to the dorsal side, with four (sometimes three) large spines which alternate in position on adjacent plates.

Description. The two specimens are ten-rayed. Most of the arms are broken off near the disc and lost. The longest arm remaining attached to a specimen is 65 mm. long ; its tip is regenerated so that its length cannot be taken as a measurement of R. The radius of the disc is about 13 mm. The arms are constricted to a width of 9·5 mm. where they join the disc ; farther out they are 13 mm. wide.

None of the paxillae of the arms are arranged in regular rows. Those near the margin are somewhat bigger than, but otherwise similar to, those in the centre. Each consists of a peripheral circle of eight to twelve widely spreading spinelets and a central spinelet, a little stouter but no longer than the peripheral ones. One of the peripheral spinelets is frequently replaced by a small bi-valved pedicellaria. There are no spino-paxillae.

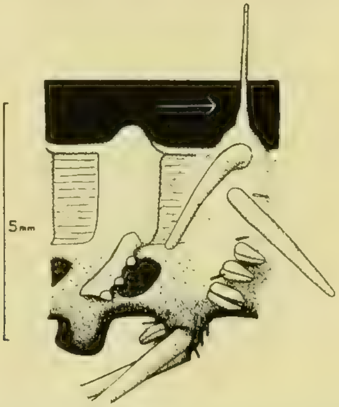

Fig. 3. *Luidia barimae* sp. n. Type. Ventral view of one side of two joints, that on the left having been denuded with sodium hypochlorite. (The arrow points towards the mouth.)

The paxillae in the centre of the disc are small and much more crowded than those of the arms. In many the central spinelet is missing. Nearly every paxilla is supplied with a pedicellaria, while many have two. The pedicellaria sometimes arises from near the centre of the paxilla.

The madreporite is 2·5 mm. in diameter and may be trefoil-shaped ; it arises from very near the edge of the disc. A few paxillae appear to arise from it, but in reality project from between the lobes, not from the madreporite itself.

The bigger elements in the armature of the adambulacral, ventro-lateral and infero-marginal plates form one continuous transverse line from the furrow to the abactinal surface. The adambulacral armature consists of spines and pedicellariae.

There is a strongly curved furrow spine, about 3 mm. long; it is compressed to a blade-like form and its end is blunt. It is followed by another blunt compressed spine which is broader and may be longer, up to 4·5 mm. long; it may be bent at its base but is thereafter straight. There is a third spine which is nearly as long but much narrower, being only slightly compressed. A few spinelets usually arise from near the base of this spine on the adoral side. There may be a fourth and smaller spine borne on the inner end of the ventro-lateral plate, but it is usual for these plates to carry two or three large bi-valved pedicellariae, of which the outermost, about 1 mm. long, is larger than the inner ones. Small spinules may arise around the base of the pedicellariae, especially, in the proximal part of the arm, where there may even be four rather than three pedicellariae on each plate; in the distal part of the arm there is only one. There are no pedicellariae in the furrow as are found in *L. avicularia* and *L. integra*.

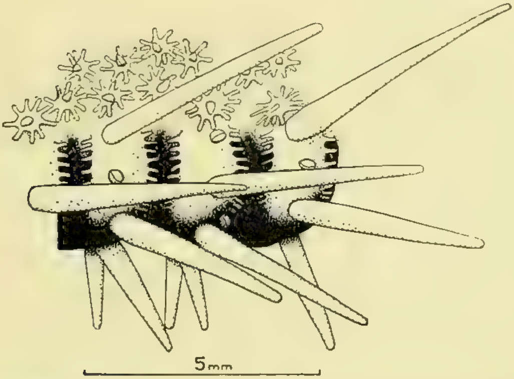

FIG. 4. Dorso-lateral view of three infero-marginal plates and the adjacent paxillae.

The infero-marginal plates encroach strongly on the abactinal surfaces of the arms. They are raised into strong ridges. In the proximal part of the arm there are four large spines on each plate. Three are on the lateral edge, one above the other, the lowermost shorter than the second and third which may be 6 mm. long. The fourth and longest spine, up to 8 mm. long, arises from or near the inner edge of the plate on the abactinal surface. The spines of adjacent plates arise at different levels as a rule, so that the uppermost spine of one plate is based on the extreme adradial edge, while that of the next plate is somewhat inset, the lower spines being correspondingly displaced on every second plate. On each row of infero-marginal plates there are thus eight series of spines, those of any one series all arising at the same level and usually only occurring on alternate plates. On those plates where the uppermost spine is not on the extreme inner edge of the plate there may be only three spines in the distal part of the arm. Numerous spinules occur in a thick row on the proximal and distal edges of the infero-marginal plates; they point into the furrows between the plates. One or two small bi-valved pedicellariae occur on most of the plates, often on the innermost abactinal edge when there is no spine in that position.

Pedicellariae are numerous on the jaws and in the small interradial areas.

The colour of the spirit specimens is greyish-brown above, light below.

REMARKS. This species appears to be most nearly related to *Luidia heterozona* Fisher from West Africa (of which *L. mortenseni* Cadenat is a synonym), although that species is included by Fisher (1940 : 268) in the *Ciliaris* group since its superomarginal plates are markedly larger than the adjacent lateral paxillae.

Döderlein's genealogical tree (1920 : 223) indicates that the *Ciliaris* group is very closely related to the subgenus *Integraster* of the *Quinaria* group (in which *L. barimae* seems to belong), and indeed *Luidia heterozona* is as much, if not more, in accord with the ten-rayed *Quinaria* group species such as *L. integra* Koehler, *L. avicularia* Fisher and *L. moroisoana* Goto as with the other species of the *Ciliaris* group, none of which has more than eight arms. In the subgenus *Integraster* the supero-marginal paxillae are larger and fewer in number than the adjacent rows of paxillae, even it not so conspicuously different as in *L. heterozona*. In *L. barimae* the lateral paxillae are much more irregularly arranged.

The only other notable difference between *L. heterozona* and this new West Indian species is in the number of infero-marginal spines, of which there are commonly four on each plate in *L. barimae* but only two or three in *L. heterozona*, although the conspicuous alternation in the position of these spines is similar. The number of pedicellariae between the outermost adambulacral spine and the lowermost inferomarginal one may be as many as three in some specimens of *L. heterozona* according to Madsen (1950 : 204), although the number is usually one. On the whole it seems better to regard *Luidia heterozona* as also belonging to the *Quinaria* group, it being the east Atlantic counterpart of *L. barimae*. Whether the differences between the two are less than specific, as with the east American *Luidia alternata* and its subspecies *numidica* from West Africa, remains to be seen from a greater range of West Atlantic material, showing the variation particularly of the armature of the infero-marginal and ventro-lateral plates.

The Indo-Pacific species *Luidia integra*, *L. avicularia* and *L. moroisoana* are easily distinguished from *L. barimae* by the possession of spino-paxillae, and in having a long-jawed pedicellaria within the furrow on the adambulacral plates.

Family GONIASTERIDAE

Ceramaster granularis forma ***balteatus*** (Sladen)

Pentagonaster balteatus Sladen, 1891 : 688, pl. 25, figs. 1–5.
Pentagonaster hystricis von Marenzeller, 1893 : 4, pl. 1, fig. 2, pl. 2, fig. 2 ; Ludwig, 1897 : 179, pl. 8, fig. 2.
Pentagonaster gosselini Perrier, 1894 : 399, pl. 26, fig. 4 ; 1896 : 45 ; Koehler, 1909 : 84, pl. 1, fig. 9.
Pentagonaster kergroheni Koehler, 1896 : 63, pl. 2, figs. 8–10.
Ceramaster balteatus, Mortensen, 1927 : 82, text-fig. 45.
? *Pentagonaster haesitans* Perrier, 1894 : 397, pl. 23, fig. 7, pl. 25, fig. 2.

St. 49. 28° 25′ N., 13° 34′ W. (between Fuerteventura Island and Africa); agassiz trawl; *c.* 1300 m. Nine small specimens.

The typical north-European form of *Ceramaster granularis* (Retzius), from depths as shallow as 20 metres, is nearly pentagonal in outline, with the short triangular rays projecting abruptly. The R/r ratio equals *c.* 1·3 to 1·5/1, rarely more. The marginal plates of both series each have a bare patch, which is relatively larger in the young sea-star. There are usually three or four short, thick furrow spines and two, sometimes three, shorter spines in the second row backed by several rows of granules. The variations have been studied in detail by Grieg (1907 : 22—32, text-figs. 1 and 2). It has been reported from off Morocco by Perrier and from the east coast of North America by Sladen and Verrill.

From south-west of Ireland to north-west Africa and the Mediterranean, at depths of more than 1,000 metres, is found a relatively longer-armed form with R/r averaging 1·7/1 and with the interbrachial arcs regularly curved, not angular. The marginal plates are more or less completely covered with granules and the furrow spines number from four to six on each adambulacral plate, with three spines in the second series backed by granules.

Several names have been given to such specimens, of which *Pentagonaster balteatus* Sladen has priority. Sladen's type was dredged in 750 fathoms (1,372 metres) in 51° 01′ N., 11° 50′ W. (south-west of Ireland). It has all the marginals completely covered with granules, R/r = 1·7/1, and there are six furrow spines on each plate, the adoral one being inset and shorter than the others.

Perrier originally described *Pentagonaster gosselini* as having only three or four furrow spines, but later (1896) mentions specimens with four to six adambulacral spines. The supero-marginal plates may be covered with granules or have bare patches according to Koehler (1909); Perrier says that their granulation is "fugace."

"*Pentagonaster*" *kergroheni* Koehler from the Bay of Biscay in 1,710 metres has only the distal supero-marginals with a small bare patch free of granules. R/r = 1·7/1 and there are five furrow spines. Ludwig (1897) declares that *P. kergroheni* is a synonym of *P. hystricis* von Marenzeller from the Mediterranean, which may also have small bare patches on the marginal plates. This seems very likely, although the Mediterranean form apparently has the granulation more spaced out than in Atlantic specimens. However, Ludwig is mistaken in thinking that *P. concinnus* Sladen and *P. greeni* Bell might also be synonyms of *P. hystricis*, for the former having only marginal granules on the dorsal plates is synonymous with *Plinthaster perrieri* (Sladen) as other authors have pointed out, while *P. greeni* does not have tabulate dorsal plates and like *Ceramaster placenta* (Müller & Troschel) might be referred to *Peltaster* Verrill.

Ludwig also says that older specimens of *P. hystricis* tend to have more numerous and larger bare patches on the marginals than young ones, which is the converse of what occurs in typical *granularis*. However the "Rosaura" specimens, the largest of which has R only 15 mm., all have bare patches on the supero-marginals and five of them on all the infero-marginals also. The other four, including the largest one, have the proximal infero-marginals completely covered with granules, and only the last two or three have a small bare patch. The R/r ratio varies between

1·45 and 1·7/1, averaging 1·6. The width of the marginals also seems to vary with the length of the arms, as they are broader when the shape is more pentagonal.

As for North American specimens of *Ceramaster granularis*, those collected by the "Challenger" south of Halifax, Nova Scotia, in 156 metres, differ little from the north European form except in having relatively longer arms, so that R/r averages 1·7/1. "*Pentagonaster*" *eximius* Verrill (1895) is a synonym of *Ceramaster granularis*, for Verrill's conception of the latter obviously approximates more to *balteatus* than to the typical form, as can be seen from his comparison. It seems quite probable that a longer-rayed form somewhat similar to *balteatus* occurs beside the typical one on the east coast of North America, just as typical *granularis* is found off North Africa according to Perrier, as well as the longer-armed form.

Family Brisingidae

St. 26. 17° 53′ N., 87° 44′ W. (off British Honduras); agassiz trawl; *c.* 900m. One damaged arm fragment consisting of 46 joints, 95 mm. long.

At one end of the fragment the first and second adambulacral ossicles have, lying above and fused to them, two marginal plates, showing that this is the proximal part of an arm. The first marginal plate on one side is the same size as that on the other. The first two pairs of ambulacral plates are shorter than the remainder, which are each about 2·25 mm. long. The soft tissue is stripped off the first seven joints, but some remains on the dorsal side between the eighth and the sixteenth joints. Five costae, consisting of light ossicles with no spines, occur in that interval, that is, one to about every two joints. Beyond the sixteenth joint the arm consists of ambulacral and adambulacral ossicles, spines and shreds of tissue.

Each of the adambulacral ossicles carried a moderate-sized spine on its lower edge, a little nearer to the distal than the proximal end. Larger spines than these arise from the distal end of the outer edge of the adambulacral ossicles beyond the seventh; they appear to occur, with slight irregularities, on alternate ossicles. None is complete, the longest remaining being about 4·5 mm. long. The skin coverings of most are torn off but they are covered with numerous small crossed pedicellariae.

We cannot with confidence assign this fragment to any of the three species of the Brisingidae known from the Caribbean region: *Hymenodiscus agassizi* Perrier, *Odinia antillensis* A. H. Clark and *Freyella mexicana* A. H. Clark. What remains of the adambulacral spines are unlike those described for *O. antillensis* and *F. mexicana*. They are not unlike those of *H. agassizi*, and the structure of the arm is very like what Perrier describes for that species (1884: 189, pls. 1 and 2): the ambulacral ossicles have an exactly similar process for articulation with the adambulacral ossicles. Fisher (1918: 104, figs. 1 and 2) describes how the first marginals of *H. agassizi* which meet in an interbrachium are unequal in size. The first marginals of this single arm are of equal size; it may be that each met in its interbrachium a smaller first marginal. Fisher found that the abactinal integument of the rays of *H. agassizi* contained holothuroid plates. There are none in this specimen; there are on the other hand a number of light costae.

Brisingella coronata (G. O Sars)

Brisinga coronata G. O. Sars, 1871 : 5 ; 1875 : 1.

St. 49. 28° 25′ N., 13° 34′ W. (between Fuerteventura Island and Africa) ; agassiz trawl ; *c.* 1300 m. One disc.

The disc is of a young specimen, for it is only 12 mm. in diameter and the spines on its abactinal surface are fine and fairly far apart. There were eight arms.

Family ASTERIIDAE

Stephanasterias albula (Stimpson)

Asteracanthion albulus Stimpson, 1853 : 16, pl. 1, fig. 5.
Stephanasterias albula Heding, 1935 : 38.

St. 6. 60° 06′ N., 45° 25′ W. (off S.W. Greenland) ; three-feet dredge ; 110 m. Two specimens.

At first sight the larger specimen with R = 11 mm. appears to be five-rayed, but one of the larger arms has a very short arm coalesced with its proximal portion. The smaller specimen is six-rayed.

Class OPHIUROIDEA

Family OPHIACANTHIDAE

Ophioplinthaca grenadensis sp. n.

(Text-figs. 5–7.)

St. 34. 12° 05′ N., 61° 49′ W. (off St. George, Grenada) ; agassiz trawl ; 720–800 m. One specimen.

DIAGNOSIS. A species of *Ophioplinthaca* with oval, medium-sized, bare, radial shields ; long, tapering, rugous disc-spines not concealing the scales (at least in a dry specimen) ; the dorsal arm-plates triangular, the first two barely in contact (when the disc diameter is 5 mm.), the rest separate ; arm-spines flattened serrulate, five in number ; five acute oral papillae each side of each mouth angle ; adoral shields barely meeting interradially, but with a distal lobe separating the first lateral arm plate from the oral shield ; one large, oval, tentacle-scale throughout.

DESCRIPTION. The single specimen is dried and is rather twisted. Being dry the outlines of the plates show up more than in a spirit specimen. The disc diameter is 5 mm.; there are five arms about 27 mm. long. The disc appears to be slightly indented in the interbrachial spaces. It is covered with large scales from most, if not all, of which arise strong glassy spines about 0·5 mm. long ; they are thick at the base but rapidly taper, sending off smaller spines on all sides and ending in two or three thorns. The radial shields are moderately large, naked, convex and about 1 mm. long. They are separated from one another by a wedge of scales bearing spines ; the wedge narrows from three scales within to one without.

The first two dorsal arm-plates are just in contact with one another, but beyond the second one the plates become more and more widely separated from one another. They are of a simple triangular shape, about as wide as long, with a sharp angle within, quite straight lateral edges and a gently curved distal edge. The side-plates are large and raised into strong spine-ridges. Those of the distal segments are very long.

There are five glassy arm-spines, increasing in length from the lowermost, which is as long as one segment, to the uppermost, which may be as long as two segments. They are of a characteristic shape, being flattened with each of the two blade-like edges produced into a row of teeth. The dorsal ones taper to a blunt end but the ventral spines have the end truncated, each corner being produced into a tooth.

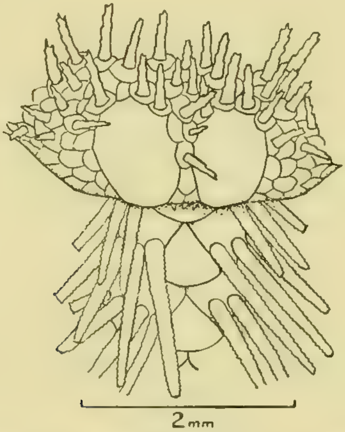

FIG. 5. *Ophioplinthaca grenadensis* sp. n. Type. Dorsal view of the base of an arm and part of the disk.

The proximal ventral arm-plates are just separated from one another; those at the end of the arm are very widely separated. They are five-sided. The two straight or slightly concave proximal sides form an angle; the lateral sides are deeply concave; the distal edge is widely rounded. The proximal plates are slightly broader than long; those further out on the arm are longer than broad.

The tentacle-scale is single and very large. It is leaf-like with a rounded free end on the proximal segments, a more pointed end on the distal segments.

The interbrachial spaces on the ventral side are covered with large, overlapping scales without spines. The oral shields are shaped like a broad spear-head, about as wide as long. The proximal sides are slightly convex, the distal concave; the distal angle is much more broadly rounded than the proximal. The adoral shields are tri-lobed. The long inner lobe narrows to a point which may be just in contact with its fellow. The outer lobes separate the oral shield from the first lateral arm-plate.

There are five or six similar triangular oral papillae on each side of the jaw and one much larger, below the teeth, at the apex.

The colour of the preserved specimen is white.

Remarks. Having the radial shields not bar-like but oval and naked, this species cannot be included in the genus *Ophiacantha* in the restricted sense. It seems to fall within the group of genera *Ophiomitrella*, *Ophiophthalmus* and *Ophioplinthaca* by virtue of the armature of the mouth-plates and the more or less distinct disc scales.

It is distinguished from *Ophiomitrella* Verrill (1899*a* : 332) by the presence of distal lobes to the adoral shields interposed between the first lateral arm-plates and the oral shields. Koehler (1922 : 124) has separated off the two species which show this character from the rest of the genus *Ophiomitrella* by creating a new genus *Ophiomelina*. However, these two species have such insignificant radial shields that they are obviously not congeneric with this new species. *Ophiophthalmus* Matsumoto has been limited and redefined by Koehler (1922 : 121), who relegated some of the species to *Ophiomitrella* and others to *Ophiomelina*. None of the species left in *Ophiophthalmus* has a distal lobe to the adoral shields, which instead meet widely interradially although *Ophiophthalmus hylacantha* (H. L. Clark 1911 : 227) does have thorny tapering disc-spines, arm-spines, radial shields, ventral arm-plates and tentacle-scales very like this new species.

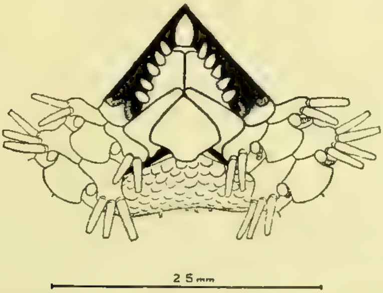

Fig. 6. Ventral view of an interbrachial angle and the bases of the two adjacent arms. (Some of the tentacles are drawn in.)

Ophioplinthaca Verrill (1899*a* : 351), which grades into *Ophiomitrella*, includes forms with oral papillae in a simple series, a single apical papilla, relatively large bare radial shields and the disc notched interradially usually with specialized marginal scales. Except for the last character, which is indistinct in the immature specimen of *O. grenadensis*, it conforms quite well to the other species of *Ophioplinthaca*. However most of these, like *Ophiomitrella*, have the adoral shields lacking a distal lobe between the first lateral arm-plate and the oral shield. *Ophioplinthaca partita* (Lütken & Mortensen 1899 : 179), from the west coast of Mexico, included in this genus by H. L. Clark in 1915, differs from the rest in this respect. It seems to be congeneric with this new species which is accordingly placed in the genus *Ophioplinthaca.*

Within the genus, *Ophioplinthaca rudis* (Koehler) (1922 : 142, pl. 96, fig. 1) has disc-spines which are just like those of *O. grenadensis*, although their occurrence is very variable and they may be completely absent, as illustrated by Koehler. From *Ophioplinthaca incisa* (Lyman 1883), also taken at station 34, this new species differs most obviously in having relatively smaller adoral and larger oral shields, more numerous and spaced oral papillae, single tentacle-scales on the first pores and much finer thorns on the arm-spines.

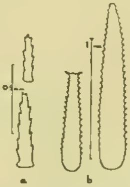

FIG. 7. *a*, Two spinelets from the disk, and *b*, a short blunt lower arm-spine and a long upper one.

The genus *Ophioplinthaca* is also characterized by the presence of broad dorsal arm-plates which are in contact in the proximal part of the arm of the adult. However, the relatively small plates of *O. grenadensis* may also be shown by young specimens of the other species of comparable size. This is illustrated in Koehler's photographs of *Ophioplinthaca globata* (1922), from the Philippine area.

The saw-like arm-spines are similar to those of *Ophiacantha hirsuta* Lyman (1875) as well as to the spines of Verrill's genus *Ophiopristis* although that genus is also characterized by the complex oral armature with several apical papillae.

In the present state of the family Ophiocanthidae the generic positions of many species are open to some doubt and a thorough revision is needed to clear up the limits of the genera.

Family OPHIACTIDAE

Ophiactis abyssicola (Sars)

Amphiura abyssicola Sars, 1861 : 18, pl. 2, figs. 7–12.
Ophiactis abyssicola, Ljungman, 1867 : 324.

St. 49. 28° 25′ N., 13° 34′ W. (between Fuerteventura Island and Africa); agassiz trawl; *c.* 1,300 m. Ten specimens.

A note by Mr. Colman on the original label describes the arms as scarlet and the body slaty-blue in life. Most of the specimens were on sponges, but it is not known whether this is a natural association or one which came about in the trawl. The disc of the largest is 7 mm. in diameter.

Family AMPHIURIDAE

Amphipholis gracillima (Stimpson)

(Text-fig. 8).

Ophiolepis gracillima Stimpson, 1852 : 224.
Amphipholis gracillima, Ljungman, 1867 : 314.

St. 22. 17° 28′ N., 88° 11′ W. (Belize Harbour, British Honduras) ; two-feet dredge ; 6 m. Six specimens.

Most of Stimpson's original specimens had lost their discs, as three of the present specimens have done . None has complete arms but many long fragments remain, and where they are fractured they show no sign of tapering to an end.

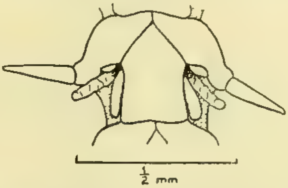

FIG. 8. *Amphipholis gracillima* (Stimpson). Ventral view of a middle arm segment.

The species does not appear to have been described as possessing tentacle-scales. The present specimens have two, a long narrow inner scale reaching slightly further than the segment to which it belongs, and a small outer scale.

One specimen sent to the late Dr. H. L. Clark of the Museum of Comparative Zoology, was compared by him with a specimen of the same size from Tobago and with one of the types of *Amphipholis gracillima*. He thought there was no doubt that the " Rosaura " specimens belong to this species, but their tentacle-scales, particularly the inner, are bigger than in the type and the Tobago specimen. They are accordingly figured here.

The specimens retain in spirit bars of a rich reddish colour at the distal end of each arm-segment on the underside.

Family OPHIOCHITONIDAE

Ophionereis dolabriformis[1] sp. n.[2]

(Text-figs. 9–11).

St. 35. 9° 25′ N., 59° 52′ W. (off the mouth of the river Orinoco) ; otter trawl ; 86 m. One specimen.

DIAGNOSIS. A species of *Ophionereis* with very fine disc-scales, becoming a little larger around the radial shields ; supplementary dorsal arm-plates very small

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[1] *dolabriformis* = axe-shaped, referring to the ventral arm-plates.

[2] Owing to delay in publication of this paper a brief description of this species has already appeared in print. (A. M. Clark, 1953, A Revision of the genus *Ophionereis*. *Proc. Zool. Soc. Lond.* 123 : 65–94.)

and limited to the distal half of the joint, even on the proximal segments ; three long, tapering arm-spines which vary irregularly in relative length, the uppermost usually the longest, sometimes exceeding one-and-a-half times the length of the corresponding joint, the middle one sometimes the shortest but often all three about the same length ; adoral shields barely meeting interradially and also narrow outwardly, being overlapped by the oral shield which, at its widest part just reaches the first lateral arm-plate on each side ; disc coloured with very compact dark reticulations.

Description. The specimen has been dried and the disc has perforated centrally so that the teeth are visible from the dorsal side through the gap. It has contracted considerably in the interradial areas so that the diameter is hard to measure ; it is about 8 mm. All the arms are broken, the longest remaining being about 40 mm. in length and still quite stout at the end of that distance, the total length being probably in the region of 70 mm.

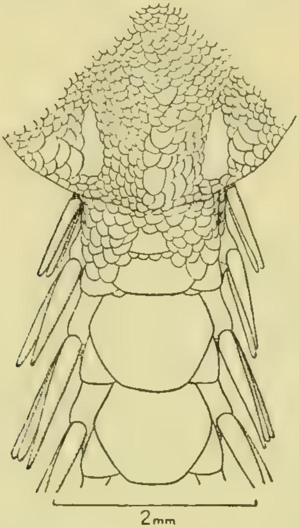

Fig. 9. *Ophionereis dolabriformis* sp. n. Type. Dorsal view of the base of an arm and part of the disk.

The disc scaling is fine but a little coarser around the radial shields, a few of the mid-radial scales being enlarged also. On the ventral side it is fairly uniform up to the genital slits, which lack papillae. The scaling extends out on to the dorsal side of the arm-bases for several segments.

The dorsal arm-plates are hexagonal in shape, the widest part being about the middle. The two latero-proximal sides are in contact with the lateral arm-plates, while the latero-distal sides (which usually curve round into the distal side) are bordered by the short supplementary arm-plates, which are triangular with a curved distal edge.

The lateral arm-plates bear three long, needle-like, tapering spines of varying relative length ; they may all be equal, or the uppermost may be longest and the middle one shortest, or the uppermost may be the shortest and the other two about equal. Their maximum length exceeds one-and-a-half times the length of the corresponding joint.

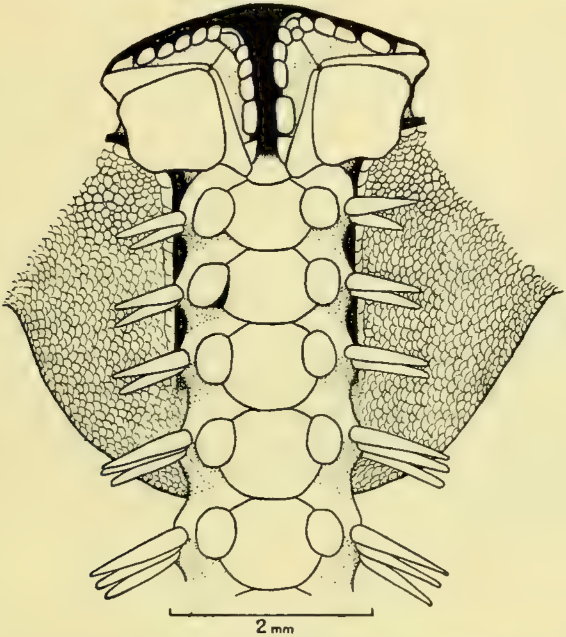

FIG. 10. Ventral view of the base of an arm and the adjacent interradial areas.

The ventral arm-plates are shaped like a battle-axe head, with the distal edge very convex and a little wider at the distal end of the tentacle-scales than proximal to them. (This form might also be interpreted as " bell-shaped "). After the first few the plates are a little longer than wide.

There is one large, oval tentacle-scale completely covering each pore.

The oral shields are broadly spear-head-shaped, the widest part being towards the distal end and the two nearly straight proximal sides meet at an angle, while the shorter distal sides are each slightly concave across the head of the genital slit but form a blunt distal angle. The adoral shields are not very large and are completely overlapped by the oral shields at their widest point. Internally they just meet inside all the oral shields except the madreporite, which is a little larger and is swollen. There are four or five oral papillae on each side, the outermost being the largest when they are four; on some angles there is a small apical papilla, but on others the lowest tooth is clearly visible. Beyond the outermost papilla is an oral tentacle-scale.

The disc is marked with very close dark reticulations, much more compact than those of *O. reticulata*. On the arms at intervals of three or four segments there are brownish-purple bands, each extending for one-and-a-half segments. Besides these there are fainter markings elsewhere on the dorsal sides of the arms, including an ill-defined longitudinal line down the centre of the arm.

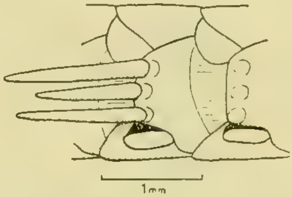

FIG. 11. Lateral view of part of an arm.

REMARKS. The other three West Indian species of *Ophionereis* are *O. reticulata* (Say), which is very common, *O. squamulosa* Koehler, known from St Thomas, Parahiba in Brazil and common at Tobago and the Tortugas according to Dr. H. L. Clark, and finally *O. olivacea* H. L. Clark, known only from two specimens, from Porto Rico and Florida. Dr. Clark has given a key to the identification of these (1933 : 39). *Ophionereis dolabriformis* differs from the first two named above by its small supplementary arm-plates and from all three by the needle-like arm-spines and the coloration of the disc.

Family OPHIOLEPIDAE

Amphiophiura metabula H. L. Clark

Amphiophiura metabula H. L. Clark, 1915 : 311, pl. 17, figs. 1–3.

St. 26. 17° 53′ N. 87° 44′ W. (off British Honduras); agassiz trawl; *c.* 900 m. Four specimens.

St. 34. 12° 05′ N., 61° 49′ W. (off St. George, Grenada); agassiz trawl, 720–800 m. Two specimens.

The largest have discs 8 mm. in diameter. They agree in every way with Clark's photographs except that the arm-spines are only four, or on the proximal segments five, in number, and that they are widely separated and of minute size—less conspicuous than in Clark's picture. Where there are four, the lowermost is close against the tentacle-scales, the uppermost close to the dorsal plate; the other two are so placed that the distance between all four spines is equal, or so that the distance between the middle two is slightly greater than that between the first and second and between the third and fourth. Clark's fig. 3 shows at least six arm-spines, close against one another and occupying the whole distal edge of the lateral plate.

There are two specimens in the British Museum collection which were labelled *Ophioglypha variabilis* from " Blake " station 227, 573 fathoms (1,048 metres) off St. Vincent. They of the same size as the " Rosaura " specimens and agree with them in every way, including the arm-spines.

Ophiomusium validum Ljungman

Ophiomusium validum Ljungman, 1871 : 618.

St. 26. 17° 53′ N., 87° 44′ W. (off British Honduras) ; agassiz trawl ; *c.* 900 m. Sixty-five specimens.

The diameter of the disc is up to 10 mm., which is greater than Lyman gives. There is a far larger specimen, diameter 17 mm. among three in the British Museum from " Blake " station 238, 127 fathoms (232 metres) in the Grenadines. Lyman (1878, pl. 1, fig. 9) shows four equally spaced arm-spines. Most of the present specimens and some of the " Challenger " ones in the British Museum collection have only three spines, the third (the highest) a greater distance from the second than the second is from the first. Some have four spines at the base of the arms, as the " Blake " specimens do ; the two lowermost spines are closer together than the second and third and the third and fourth.

Minute ventral arm-plates are present for a short distance beyond the third segment ; they persist a long way out in the large " Blake " specimens.

The radial shields are usually contiguous without, but they are sometimes completely separated as in the large " Blake " specimens.

Family OPHIOLEUCIDAE

Ophiernus adspersus Lyman

(Text-fig. 12)

Ophiernus adspersus Lyman, 1883 : 236, pl. 3, figs. 19–21.

St. 26. 17° 53′ N., 87° 44′ W. (off British Honduras) ; agassiz trawl ; *c.* 900 m. One specimen.

St. 34. 12° 05′ N., 61° 49′ W. (off St. George, Grenada) ; agassiz trawl, 720–800 m. Five specimens.

The six rather broken specimens from this collection and two co-types in the British Museum from " Blake " station 185, Dominica, 333 fathoms (610 metres), all show a character which has not been described in this species or in any other of the genus. A single closely placed row of fine glassy bristles arises from the distal

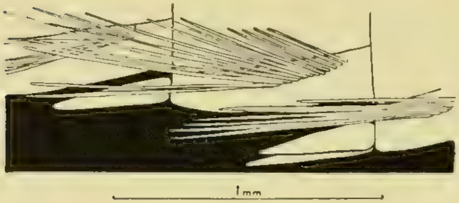

Fig. 12. *Ophiernus adspersus* Lyman. Dorsal view of part of an arm to show the bristles on the lateral arm-plates.

edges of the side plates on the dorsal side of the arm. In the proximal part of the arm they are slightly longer than an arm joint ; farther out on the arm they are longer.

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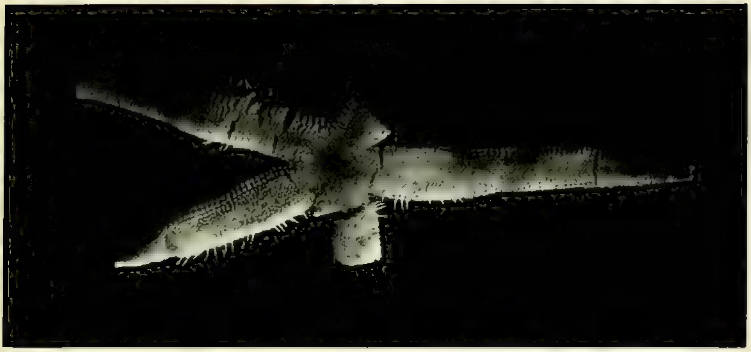

FIG. 1

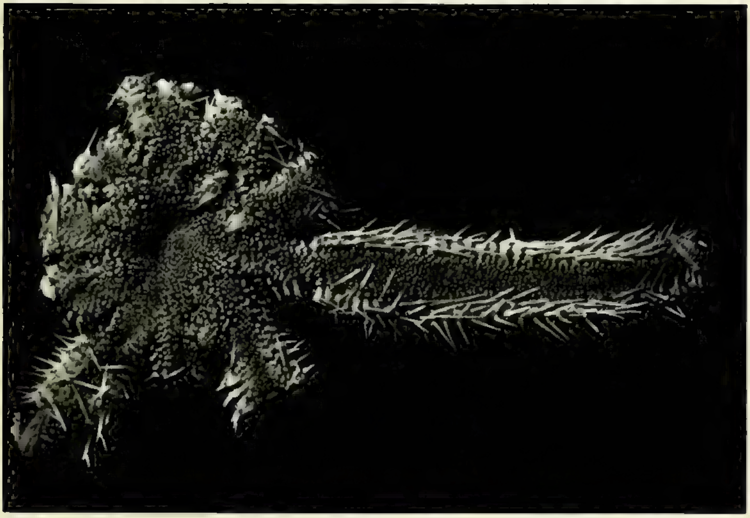

FIG. 2

Plate 6, fig. 1. *Luidia rosaurae* sp. n. Type. Dorsal view. Fig. 2. *Luidia barimae* sp. n. Type. Dorsal view. Both natural size.

4. REPORT ON THE FISHES COLLECTED BY S.Y. "ROSAURA" IN THE NORTH AND CENTRAL ATLANTIC, 1937-38

PART 1. FAMILIES CARCHARHINIDAE, TORPEDINIDAE, ROSAURIDAE (NOV.), SALMONIDAE, ALEPOCEPHALIDAE, SEARSIDAE, CLUPEIDAE

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British Museum (Natural History)

[*Received 25th April,* 1953]

With Plates 7 and 8 and Text-figs. 1-19

SYNOPSIS

Specimens of *Carcharhinus leucas* (Müller & Henle); *Diplobatis pictus* Palmer; *Rosaura rotunda* nov, ; *Salvelinus alpinus* (L) ; *Leptoderma macrops* Vaillant; *Searsia koefoedi* Parr; *Persparsia taaningi* Parr; *Pellonula afzeliusi* Johnels; *Harengula pensacolae* G. & B.; and *Ilisha africana* (Bloch) are reported upon. The family *Rosauridae* is proposed for *Rosaura rotunda* nov., an aberrant new oceanic Isospondyl. The paper presents new observations and discussion of tumours in *Salvelinus;* of the structure and functions of the shoulder-organ of Searsidae; of the occurrence of lateral line papillae in Alepocephalidae; and of the general taxonomic significance of photophore systems.

INTRODUCTION

As soon as the " Rosaura " fishes were received at the British Museum (Natural History) in 1938, a preliminary rough-sorting and assessment were carried out by Lieut.-Col. W. P. C. Tenison, D.S.O., who also made illustrations of six of the more bizarre deep-sea species which were included in a popular account by J. S. Colman published as an appendix to the late Lord Moyne's *Atlantic Circle* in the same year. (Another version of the same material is included in Colman, 1950, *The Sea and its Mysteries.*) With the approach of war the collection was set aside and remained unstudied until 1951, when I began my apprenticeship in ichthyology with a very laboured consideration of it. Many of the larvae and smaller specimens were still unnamed, and for a variety of reasons it was sometimes necessary to modify Lieut.-Col. Tenison's determinations ; but his work had materially shortened the initial task of identification and is gratefully acknowledged.

The collection is especially rich in well-preserved bathypelagic species from the little-worked Caribbean and equatorial Atlantic, and the present report will lay greater emphasis upon these than upon the shore fishes.

A general list of species taken at each station will appear with the concluding instalment of the report, together with any minor addenda and corrigenda and general conclusions suggested by the work. Photographs used are acknowledged as applicable ; all other figures are from drawings by the author. Except where specially stated, standard lengths (S.L.) of fishes are given, and denote the measurement from the tip of the snout to the base of the caudal fin.

My best thanks are offered to those specialists and museum curators in other institutions whose assistance is mentioned in the text. I am especially grateful for the interest, advice and guidance so gladly given by my colleagues Dr. Ethelwynn Trewavas and Mr. N. B. Marshall, and for the services rendered by the technical staffs of the Fish Section and Photographic Studio of the British Museum (Natural History). I am indebted to Mr. J. S. Colman (now Director of the Marine Biological Station, Port Erin, I.o.M.), who made this very fine collection and has permitted the reproduction of extracts from his field notes which appear as quotations in the text.

Order PLEUROTREMI

Family CARCHARHINIDAE

Carcharhinus sp., probably ***C. leucas*** (Müller & Henle), alternatively ***C. longimanus*** (Poey) or ***C. obscurus*** (Lesueur).

(Pl. 7)

(1) ***Carcharhinus (Prionodon) leucas*** (Müller & Henle).

Carcharias (*Prionodon*) *leucas* Müller & Henle, 1841, *Syst. Besch. Plagiostomen* : 42. Berlin.
Carcharhinus leucas Bigelow & Schroeder, 1948, *Fishes of the Western North Atlantic*, **1**, Sharks : 337 ; Myers, 1952, *Copeia* : 268.

HAB. Western Atlantic, New York to Southern Brazil ; (?) Peruvian Amazon.

(2) ***Carcharhinus longimanus*** (Poey).

Squalus longimanus Poey, 1861, *Memorias hist. nat. Cuba*, **2** : 338.
Carcharhinus longimanus Bigelow & Schroeder, 1948, t.c. : 354.

HAB. Tropical and subtropical Atlantic ; Mediterranean.

(3) ***Carcharhinus obscurus*** (Lesueur).

Squalus obscurus Lesueur, 1818, *J. Acad. nat. Sci. Philad.*, **1** : 223.
Carcharhinus obscurus Bigelow & Schroeder, 1948, t.c. : 382.

HAB. Western Atlantic, New York to Florida & Bermuda ; doubtfully southwards to Brazil.

St. 41. 18.xii.37. 0° 38′ S., 43° 42′ W. 2-metre stramin net, 900(–0) metres. One specimen (a female), 211 cm. total length. Notes and photographs taken ; heart only preserved. Reg. No. 1953.3.6.1.

The following data are extracted from notes by J. S. Colman :

"Shark. Female. *Carcharhinus* sp. (acc. to Norman). Colour—grey dorsally, white ventrally. Two rows of teeth. No spines in front of fins. Ducti endolymphaticus present. 5 gill-slits each side. Stomach quite empty. Ovaries very immature ; no eggs developing. I could find no parasites. Four Remoras accompanied it."

Dimensions:

Snout to end of caudal fin (*total length*)	211 cm.	
,, mouth (middle of upper lip)	14 ,,	(6·6% T.L.)
,, eyes	15 ,,	(7·1% ,,)
,, 1st gill-slit	40 ,,	(18·9% ,,)
,, 5th ,,	53 ,,	(25·1% ,,)
,, base of pectoral fin	52 ,,	(24·6% ,,)
,, ,, 1st dorsal fin	66 ,,	(31·2% ,,)
,, cloaca	112 ,,	(53·0% ,,)
,, base of 2nd dorsal fin	132 ,,	(62·5% ,,)
,, ,, anal fin	134 ,,	(63·5% ,,)
,, ,, caudal fin	150 ,,	(71·0% ,,)
Girth at 1st gill-slit	84 ,,	
Max. girth (at base of 1st dorsal fin)	88 ,,	
Min. girth (at base of caudal fin)	27 ,,	
Spread of pectoral fins	113 ,,	

On the following characters the specimen may be assigned to the family Carcharhinidae in the sub-order Galeoidea: A normally shaped head, not laterally expanded; five gill-slits, the last situated behind the origin of the pectoral fins; two series of teeth functional; two dorsal fins, which are not preceded by spines; first dorsal much shorter at base than caudal and terminating well before the origin of the pelvics; an anal fin present; caudal fin not lunate and occupying less than half the total length.

Indirect methods of identification, taking into account the absence of a spiracle, the short snout, and the relative sizes, shapes and insertions of the fins, allow the elimination of *Galeocerdo*, *Paragaleus*, *Prionace*, *Negaprion*, *Aprionodon*, *Scoliodon* and *Hypoprion*. There remains only *Carcharhinus*, with fourteen Western Atlantic species, of which one, *C. nicaraguensis*, is confined to fresh water, and others have notably longer snouts as well as differences in the fins which are unmistakable. Of three species one " possible," *C. leucas*, seems by far the most likely.

C. leucas has the reputation, consonant with a capture in a plankton net, of being a heavy, slow-swimming species. Against an almost complete correspondence with the smaller female described by Bigelow & Schroeder, the present specimen offers only very small differences in the more posterior insertions of the pectoral and first and second dorsals, and these seem negligible when considered against small differences likely from methods of measurement and probable ontogenetic and other variations.

C. longimanus agrees in the short snout and long, slender pectoral, and in the relative insertions of the fins, but has broader 1st dorsal and ventral fins and longer posterior tips to the 2nd dorsal and anal.

C. obscurus belongs to the group of species having a median dorsal ridge, the presence or absence of which cannot certainly be determined from the photograph.

It has a short snout and other characters in common with the present specimen, but appears to differ considerably in the shorter pectoral and lower second dorsal.

The Remoras mentioned by J. S. Colman are four examples of *Remora remora* (L), 102–195 mm. S.L. In view of a very interesting paper by Szidat & Nani (1951, *Rev. Inst. Ciencias nat. y Mus. Argentino*, **2** : 385) presenting evidence that Remoras feed upon the copepod ectoparasites of sharks and other large fishes, I made a point of examining these specimens. No recognizable organisms were found in the very small amount of food present in their mouths and stomachs; the result, though disappointing, is in accord with the field-note on the absence of shark parasites.

Order HYPOTREMI

Family TORPEDINIDAE

Diplobatis pictus Palmer

(Pl. 8)

Palmer, 1950, *Ann. Mag. nat. Hist.* (12) **3** : 480.

St. 35. 1.xii.37. 9° 25′ N., 59° 52′ W.; otter trawl; 86(–0) metres. One specimen (a female), 131 mm. total length. Reg. No. 1953.3.6.2.

St. 36. 2.xii.37. 7° 11′ N., 57° 59′ W.; otter trawl, 20(–0) metres. Two specimens (females), 110–140 mm. total length. Reg. No. 1953.3.6.3–4.

HAB. Guiana Coast; mouth of R. Orinoco.

This species was previously represented in the Museum's collections by the unique holotype, Reg. No. 1950.5.15.4.

The specimen from St. 35 is badly deformed, extensive injuries to the body and pectorals having been followed by irregular healing and regeneration. Those from St. 36 (Pl. 8) agree adequately with the holotype, save that a rounder form replaces the slight narrowing of the body behind the eyes, the bodies are better nourished and the hinder edges of the pelvics have broader points. The last observation led to some conjecture whether the holotype might not be an immature male, but there is nothing else to support that view, and by analogy with other Torpedinidae recognizable claspers would be differentiated at a much younger stage.

Palmer's fig. 3, it must be noted, is very diagrammatic: the edge of the pelvic is not smooth as shown but includes three or four shallow undulations each beset with several small points, and anterior to the free hind tip there is a marked zone of fusion between the inner edge of the pelvic and the ventral surface of the tail.

Reproduction of Palmer's fig. 1 rather over-emphasizes the contrast in tone between the dark spots surrounding the light markings on the back and that of the remaining dark blotches on the body. In the smallest specimen now available the light spots on either side the back have an almost pearly whiteness which evidently becomes much clouded in ontogeny; also the tips of the dorsal fins are rounder in the young stage, as in the Pacific *D. ommata*, and become pointed with age. The remaining differences described between *D. pictus* and *D. ommata* (the genotype and only other known species) are sustained by the present material.

Bigelow & Schroeder (1948, *J. Mar. Res. New Haven*, **7** : 43) give two main characters separating *Diplobatis* from other Torpedinidae : the subdivision of the nostril into two about the middle of its length by a bridge of stiff tissue, and a relationship of tooth bands to the thick, fleshy lips such that the teeth are entirely concealed when the mouth is retracted and closed.

In consideration of the possibility of ontogenetic variation in the Torpedinidae I have examined a long series of *Narcine brasiliensis* (Olfers) down to embryos with yolk-sacs attached, and find that at all stages the nostrils are undivided, so that the condition in *Diplobatis* may be regarded as distinctive enough. Nevertheless the character is of doubtful use to the taxonomist, since only in the smallest of the present specimens is the bridge intact, and even then it can hardly be described as being of " stiff tissue " throughout ; rather does there seem to be a close approximation of a concave upper and convex lower surface with a little tenuous tissue between the two. In the remaining material it would be difficult to decide from superficial appearances whether a bridge ever existed. In the holotype (of *D. pictus*) it remains as figured only on the right side, and Mr. Palmer informs me that on the left side it was ruptured during study subsequent to his paper.

Order ISOSPONDYLI

Family ROSAURIDAE nov.

Rosaura rotunda gen. et sp. nov.

(Text-figs. 1–8)

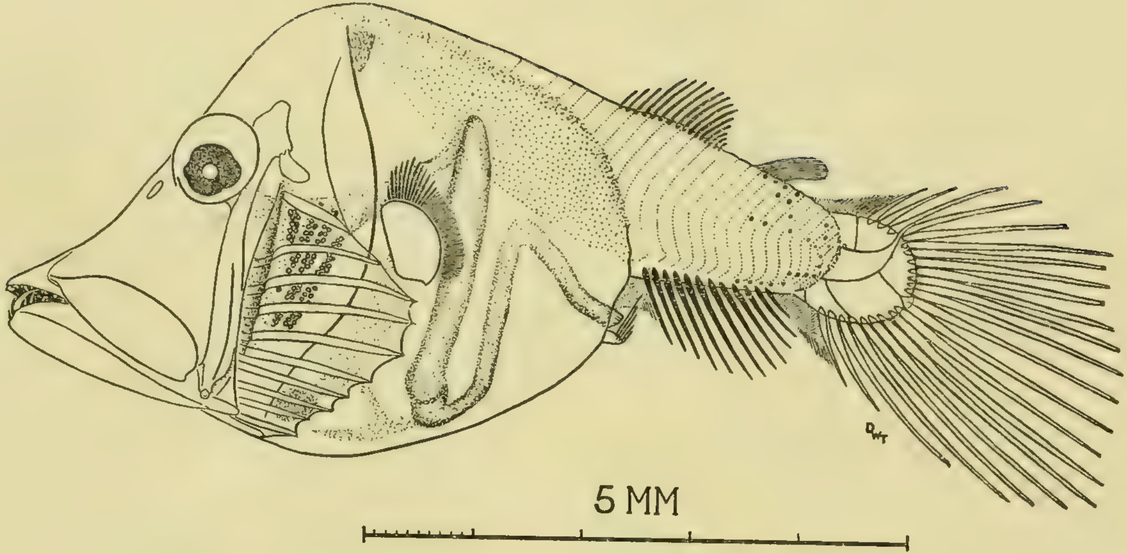
St. 42. 21.xii.37. 5° 51′ S., 34° 38′ W. ; 2-metre stramin net, 1200(–0) metres. One specimen (holotype), 8·4 mm. S.L. Reg. No. 1953.3.6.11.

HAB. Deep Atlantic, N.E. from Brazil.

Material and methods

This solitary specimen, though but a post-larva, is sufficiently advanced in ossification and general development to be recognized as substantially different from all recent and fossil Isospondyli yet known.

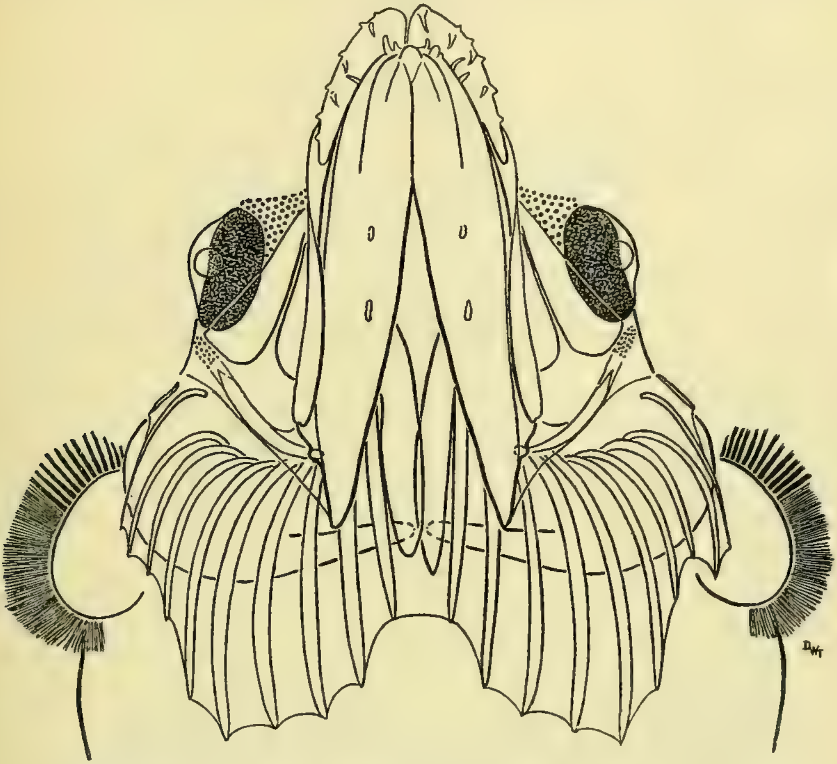
Its transparency aroused hopes of attaining a complete knowledge of the anatomy of the untreated fish, but these could not be realized fully without resort to artificial aids. I therefore made accurate notes of all structures visible in the material and then proceeded to clear and stain, controlling all stages under the microscope and employing, instead of the usual more elaborate methods (Hollister, 1934, *Zoologica*, **12** : 89–101 ; Raitt, 1935, *J. Cons. Explor. Mer*, **10** : 75–80) a simplification used in the British Museum (Natural History) for many years :



TEXT-FIG. 1. *Rosaura rotunda* gen. et sp. nov. Holotype, 8·4 mm. S.L. The specimen is shown in its condition prior to clearing and staining. Internal projection of dorsal myomeres into body-cavity shown stippled.

(1) Preserved material in 70% spirit transferred to distilled water—15 minutes.
(2) Partly cleared in 0·5% KOH solution—30 min.
(3) Stained in an old deep purple solution of alizarin in distilled water—16½ hours.
(4) 0·5% KOH solution—70 minutes. At this stage the specimen was still understained, so staining was repeated with a freshly-prepared solution.
(5) Solution of about ¼ c.c. of alizarin powder in 200 c.c. distilled water—2 hours.
(6) Solution of 2 volumes of 0·5 KOH to 1 volume of pure glycerine. During the next 24 hours glycerine was added a little at a time until the specimen could safely be transferred to pure glycerine containing a thymol crystal as preservative.

The untreated specimen had sustained compound fractures of the cleithra and wanted parts of two teeth. Processing was accomplished without further damage, but there were several breakages of caudal and branchiostegal rays during subsequent study and manipulation, which do not seem very serious in proportion to the additional information gained.



TEXT-FIG. 2. *Rosaura rotunda.* Anterior view of head from below.

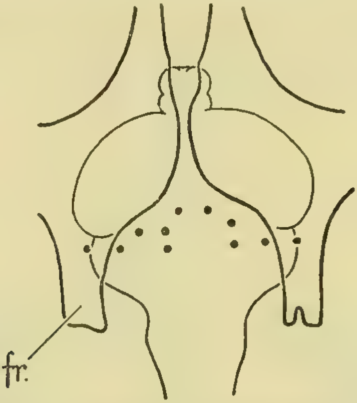
The text-figures were drawn freehand with the assistance of a 5 × 5 eyepiece graticule, calibrated with a stage micrometer.

General appearance (Text-figs. 1 and 2)

Radial formula D.16; A.12 +; C.23 +; P.12 +; V.5(L), 2(R).

Branchiostegal rays 10. Gills 4. Myomeres of body 37.

At first glance reminiscent of the larval Ceratioids, a minute fish with an overall length of 10·3 mm., transparent or translucent, scaleless and colourless save for a few isolated melanophores atop the head (Text-fig. 3) and on the caudal peduncle.



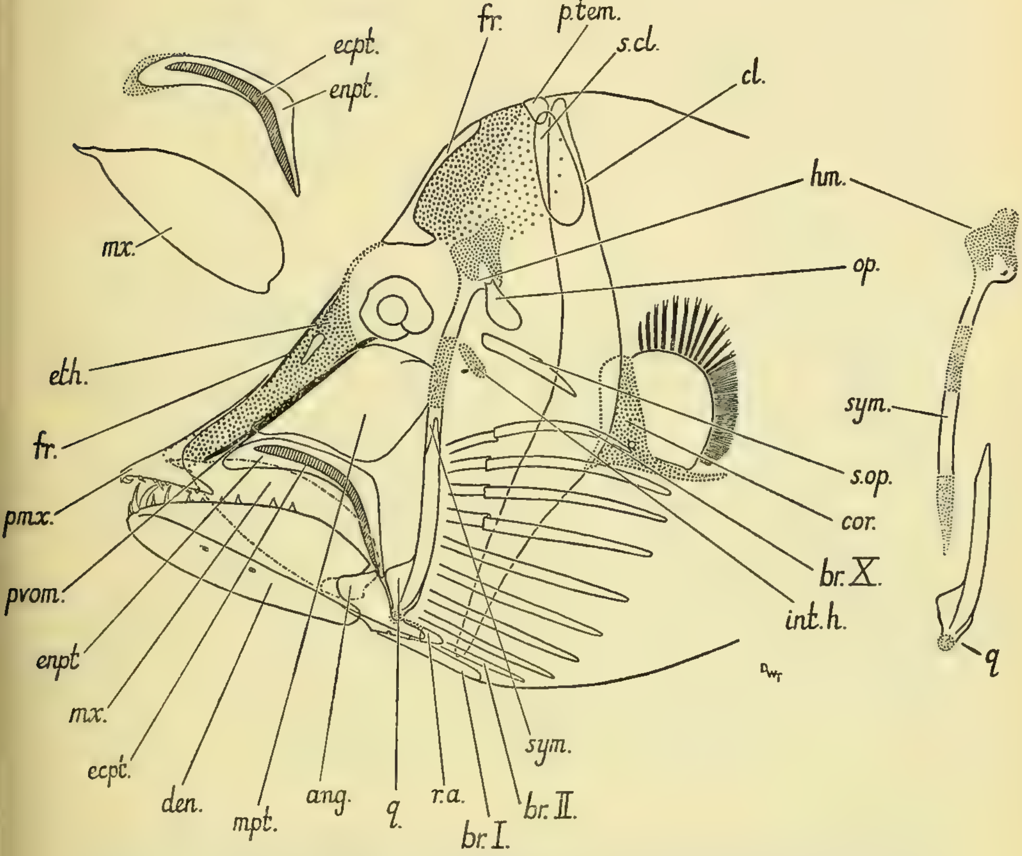
TEXT-FIG. 3. *Rosaura rotunda.* Disposition of melanophores on dorsal surface of head, shown in relation to the brain and frontal bones.

The greatest height is in the broad otic region. From this projects obliquely forwards and downwards the narrow ethmoid cartilage. The suspensorium is vertical, forming with the cranial axis and the jaws an approximately equilateral triangle. Behind this the vertebral column with its myomeres descends obliquely to the posterior end of the almost spherical body-cavity and is continued as a short caudal region.

The body-cavity is bounded in front by an almost vertically placed pectoral girdle, lightly curved forwards below, with the pectoral fins inserted about half-way in the height.

The origin of the dorsal fin is substantially in advance of that of the much larger anal. An adipose fin is present. The caudal fin is large and fan-like. A prominent anal papilla is flanked by a pair of minute abdominal pelvic fins.

The gill-openings are wide and bordered mainly by the branchiostegal membranes, which are continuous below (free from the isthmus), and supported by the much-reduced opercular and subopercular and by ten conspicuous, long, slender branchiostegal rays. Pre- and inter-opercular bones are absent. The large mouth is bordered by toothed premaxillaries and dentaries with prominent caniniform teeth. The maxillaries are toothless and probably enter the gape only to a very limited extent. The eye is small for an oceanic fish and is widely separated from the jaws. No division can be seen in either of the single pair of minute nostrils.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Text-fig. 4. *Rosaura rotunda*. Osteology of head and pectoral girdle in a cleared and stained specimen, with optical dissections of the maxillary, palato-pterygoid and hyomandibular-symplectic-quadrate. Cartilage shown stippled. For key to abbreviations used see p. 181.

Cranium (Text-figs. 4 and 7)

A great part of the cranium is still unossified, and its description limited by the difficulty of interpreting a single small and delicate specimen which may not be dissected.

The antorbital portion of the cranium is a substantial part of the whole structure. The largest element is the ethmoid cartilage, which is arched above, flat below, a long cartilage extending half the length of the head and of uncertain lateral extent. Anteriorly it is overlain by the rostral processes of the premaxillaries ; mesially it is exposed between the widely separated anterior limbs of the frontals, and posteriorly it sends thin supraorbital blades beneath the lateral processes of the frontals towards the auditory capsule. The vomer and parasphenoid are applied to its ventral surface.

The orbit is placed high on the head, laterally directed and remote from the jaws.

The postorbital portion of the cranium is an unossified chondrocranium, globose and including considerable auditory capsules. In dorsal view it is possible to see, through the frontals, edges of cartilage which run parallel and close to the optic lobes of the brain ; whether these are in fact the anterior margins of fontanelles cannot be ascertained since posteriorly they become lost in the complications of the auditory region, but it seems very likely that they are.

The only bones present on the dorsal surface of the head are the frontals, which are widely separated in the middle line. They have slender anterior extensions reaching to the tips of the premaxillary rostral processes, short posterior extensions part over the auditory capsules, and broader lateral processes contributing to the roof of the orbit. Separate parietals are not present.

The vomer (seen only in lateral view) is a narrow sliver of bone extending to beneath the anterior part of the orbit, where it overlies the front end of the parasphenoid. The latter cannot be seen distinctly and is therefore not included in any of the figures.

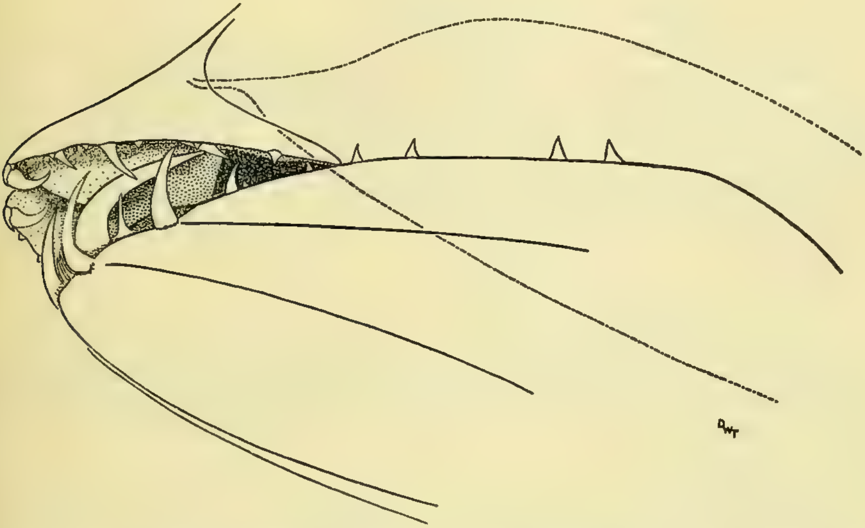
There is no mesethmoid, lateral ethmoid, or prefrontal ossified, nor are any bones of the otic or occipital series.

Jaws (Text-figs. 4, 5 and 7)

The toothed premaxillaries form the greater part of the upper boundary of the mouth. Each is V-shaped, the inner and longer arm of the V being a pointed rostral process which overlaps the anterior tip of the frontal of the same side, the outer and shorter arm being the dentigerous margin of the jaw. The premaxillaries are separated by a narrow median fissure which broadens anteriorly and posteriorly into wide notches.

The toothless maxillaries are broadly elliptical, much like those of the Sternoptychidae, and can enter but little into the gape. Each maxillary narrows anteriorly to form a twisted process inserted into the ethmoid beneath the posterior angle of the premaxillary. The squarish posterior end of the maxillary has a broad shallow notch.

Meckel's cartilage persists throughout the length of the lower jaw, though almost entirely overlain by membrane bones. The large toothed dentary is an elongated oval with a broad notch in the wide posterior end receiving, and in part overlying, the much smaller angular. There is a marked tuberosity at the mandibular symphysis. The body of the angular is roughly an equilateral triangle with the articulating facet of the quadrate above its hinder corner, and with a short narrow limb posterior to this partly overlying the end of Meckel's cartilage. The hindermost tip of Meckel's cartilage is ossified as a truncated conical retro-articular. There is no other articular ossification.



TEXT-FIG. 5. *Rosaura rotunda.* Dentition, viewed from left and slightly below. The broken line shows the position of the maxillary.

Dentition (Text-figs. 5 and 6)

The dentition is highly raptorial. The teeth on the premaxillary are in two series : an external row of seven minute teeth downwardly and outwardly directed from the edge of the premaxillary, the most anterior of the series being weakly caniniform ; and on the inner face of the premaxillary a series of four stronger, inwardly-directed and recurved teeth. The maxillary is toothless.

In the lower jaw the dentition is dominated by a pair of very large and strongly recurved caniniform teeth, set inside and a little behind the mandibular symphysis. Each dentary further carries five moderately recurved caniniform teeth of oddly-assorted sizes, and posterior to these a graded series of six to eight laterally compressed, shearing teeth. So far as may be determined without manipulating the jaws there are no vomerine teeth. (The palatines are not ossified.)

Accessory structures present in the mouth may be related to the need for removing prey impaled on the enlarged mandibular teeth. The tip of the basihyal (Text-fig. 6) bears a similar pair of enlarged and recurved teeth (one with a replacement tooth behind it), evidently capable of some degree of motion between and behind the great teeth of the mandible. Above there is a median fleshy downgrowth depending from the maxillary valve between these two pairs of teeth which may bear some functional relation to the lower dentition.

Palatine arch (Text-fig. 4 and detail)

The palatine end of the palato-pterygoid cartilage is unossified, but is not believed to be synchondrous with the lower end of the ethmoid cartilage. A broad ˥-shaped endopterygoid, rounded at its anterior end and tapering to a point at the posterior, sheaths it on its inner side. The metapterygoid is a large rhomboidal bone covering much of the cheek between the orbit and the upper limb of the endopterygoid ; its posterior end bears a suborbital prominence and is inserted mesiad to the hyomandibular-symplectic cartilage A zone of cartilage lies exposed to the surface at the periphery of the metapterygoid.

Hyoid arch (Text-fig. 4, detail and 6)

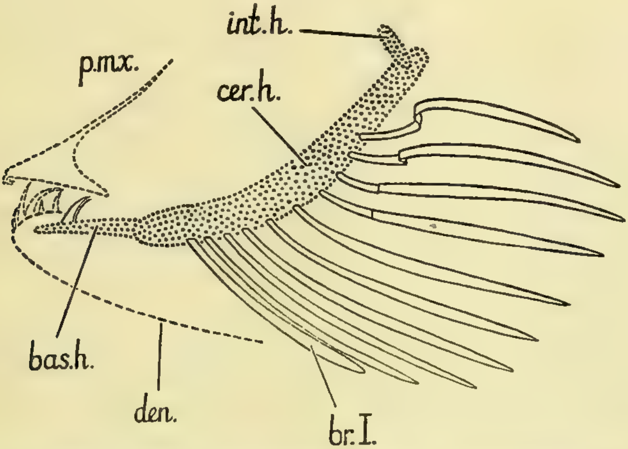
The hyomandibular is ossified only in its middle portion, the head and lower end being cartilaginous. The head comprises two dorsal protuberances (unossified) and one ventral (ossified), the latter bearing a small condyle for the articulation of the minute opercular.

The symplectic, likewise ossified in the middle portion only, is rod-shaped. Its upper end is synchondrous with the hyomandibular. Part of the ossified portion, and the whole of the lower cartilaginous end, are overlain by the quadrate.

The quadrate is a short triangular ossification, the posterior edge of which is extended upwards as a long tapering rod. The articular condyle remains cartilaginous.

The interhyal is a short cylindrical cartilage attached at its upper end to the cartilage between hyomandibular and symplectic and at its lower end to the lower limb of the hyoid arch. It is not possible to distinguish with certainty between epi-, cerato- and hypo-hyal elements, and Text-fig. 6 shows as much as can be discerned under the limitations imposed by viewing through the suspensorium and unopened jaws. The basihyal element is more readily distinguished and bears a pair of enlarged teeth.

The branchiostegal rays are long, slender, tapered towards their extremities, and elegantly curved, giving a globose contour to the anterior body of the fish. The last four describe a somewhat S-shaped curve in traversing a vertical fold of the gill-cover ; this curve is strongest in the uppermost (posterior) rays. The second to sixth rays approach the hyoid arch in a smooth simple curve. The first (lowest) branchiostegal ray is twice as broad as the rest, slightly twisted, and passes well between the rami of the mandible. The curvature and apparent grouping of the branchiostegal rays suggest, by analogy with other fishes, that there may be a ceratohyal bearing six rays and an epihyal with four.



TEXT-FIG. 6. *Rosaura rotunda.* Hyoid arch. The ten branchiostegal rays are accurately represented ; the basihyal and interhyal are also correct, but the remaining cartilages (epi-, cerato- and hypo-hyal) cannot be shown properly owing to difficulty of observation. The positions of premaxillary and dentary and of some of their teeth are shown by broken lines.

Opercular apparatus (Text-fig. 4)

The gill openings extend very nearly the full depth of the fish and are bordered by voluminous branchiostegal membranes which are continuous below (free from the isthmus). The branchiostegal membranes are supported by the opercular and sub-opercular bones and the ten branchiostegal rays ; the pointed tips of the sub-opercular and last nine branchiostegal rays project beyond the hinder edge of the branchiostegal membrane like the ribs of an umbrella ; the tips of the opercular and first branchiostegal ray do not reach to the margin of the membrane.

The opercular is a rudimentary, ventro-laterally directed, twisted, leaf-shaped bone articulating with a small condyle on the head of the hyomandibular. The sub-opercular is a narrow, pointed bone about twice as long as the preceding, converging with the tenth branchiostegal ray.

Gills and gill-apparatus

Viewed as they have been through the suspensorium, the gill-arches have yielded little information. There appear to be four only, bearing double rows of long and not very numerous gill-filaments. The lower limbs of the arches bear minute conical denticles or rakers, about a dozen to each limb.

Pectoral girdle and fin (Text-figs. 4 and 7)

The post-temporal (Text-fig. 7) is a flat, spatulate bone which mesially comes near to meeting its fellow over the otic region of the cranium, and passes almost transversely and horizontally before the dorsal somites to overly the upper tip of the supracleithrum.

The supracleithrum, so far as may be ascertained in its damaged state, is a flattened, oval bone, substantially smaller than the post-temporal; its broad postero-ventral end overlies the cleithrum a little below the latter's upper tip.

The cleithrum is very large and boomerang-shaped, and with its partner comes near to forming a complete bony ring round the body. The upper limb is nearly vertical; the lower is rather slenderer and curves forward and downward. The pectoral fin is inserted behind the posterior angle of the cleithrum at about the middle of the body-height.

The coracoid cartilage is perforated by a minute coracoid foramen and bears a prominent, posteriorly directed ventral spine, but has no trace of ossification nor of differentiation. Its anterior edge is inserted inside the hind edge of the cleithrum, and there is a small antero-ventral process which follows the edge of the cleithrum downward.

The pectoral fin of each side is much crumpled and the structure difficult to make out. Each appears to be a vertically-inserted reniform cartilaginous lobe, having no actinosts ossified as yet. Twelve adult rays have stained on the upper edge of the fin, and doubtless the number would have been increased later by the gradual replacement of the very numerous unossified larval rays.

Pelvic girdle and fin (Text-figs. 1 and 8)

There is a very slender and apparently unpaired pelvic cartilage lying transversely in the ventral body-wall before the anal papilla. The tapered ends of the pelvic cartilage turn downwards and backwards into the fin-bases; these are backwardly directed papilliform structures from which the short close-set rays project upwards and backwards. The fins are obviously in the early stages of development; that of the right side is placed higher and more anteriorly, and has but two rays compared with five on the opposite side.

Axial skeleton (Text-fig. 1)

The vertebral column is as yet entirely unossified. The surface of the stout notochord has the usual reticulate appearance; its posterior end is curved upwards and backwards and the slender tip projects between the bases of the 3rd and 4th upper caudal rays. There is a slight constriction in the notochord at the point where it breaks the edge of the fin-lobe. The first two pairs of basidorsal elements at least are laid down in cartilage (Text-fig. 7).

The dorsal fin is supported by 16 cartilaginous basalia, each of which bears one ray. The fin is smoothly rounded; the middle rays are the longest, but do not quite reach to the adipose fin when depressed. There is a wisp or two of larval ray at the hinder end, but the full adult complement seems to be present. The fin base is slightly elevated.

The adipose fin is rather large, slightly hooked, and with a fimbriated edge.

The anal fin, though probably incompletely developed, is still very much larger than the dorsal. Anteriorly there is a fringed adipose blade in which further rays might have been differentiated; there are 12 cartilaginous basalia thus far, each with a ray. The fin is rounded, the middle rays are the longest, and the depressed fin reaches to the anterior rays of the caudal. The first anal ray corresponds to the same myocomma as the eleventh dorsal ray, while the anal fin base extends beyond the posterior end of the adipose. Discussion of verticals through fin origins would be unprofitable, as may be observed from Text-fig. 1.

The caudal fin is supported by the tip of the notochord, and by two epurals and three hypurals, all cartilaginous. Between the distal extremities of the hypurals are minute triangular supplementary cartilages. There are three epaxial and twenty hypaxial rays, all elegantly curved and tapered at their extremities; the broadest part of each ray lies a short distance from its insertion, as in a quill. The dorsal rays are a little more slender and closely set than the ventral; the rays are evenly gradated and form a considerable caudal fan. Anterior to the caudal rays on both dorsal and ventral edges is a fringed adipose blade in which it is evident that a substantial number of procurrent caudal rays would have been differentiated.

Branching is incipient at the ends of most of the fin-rays.

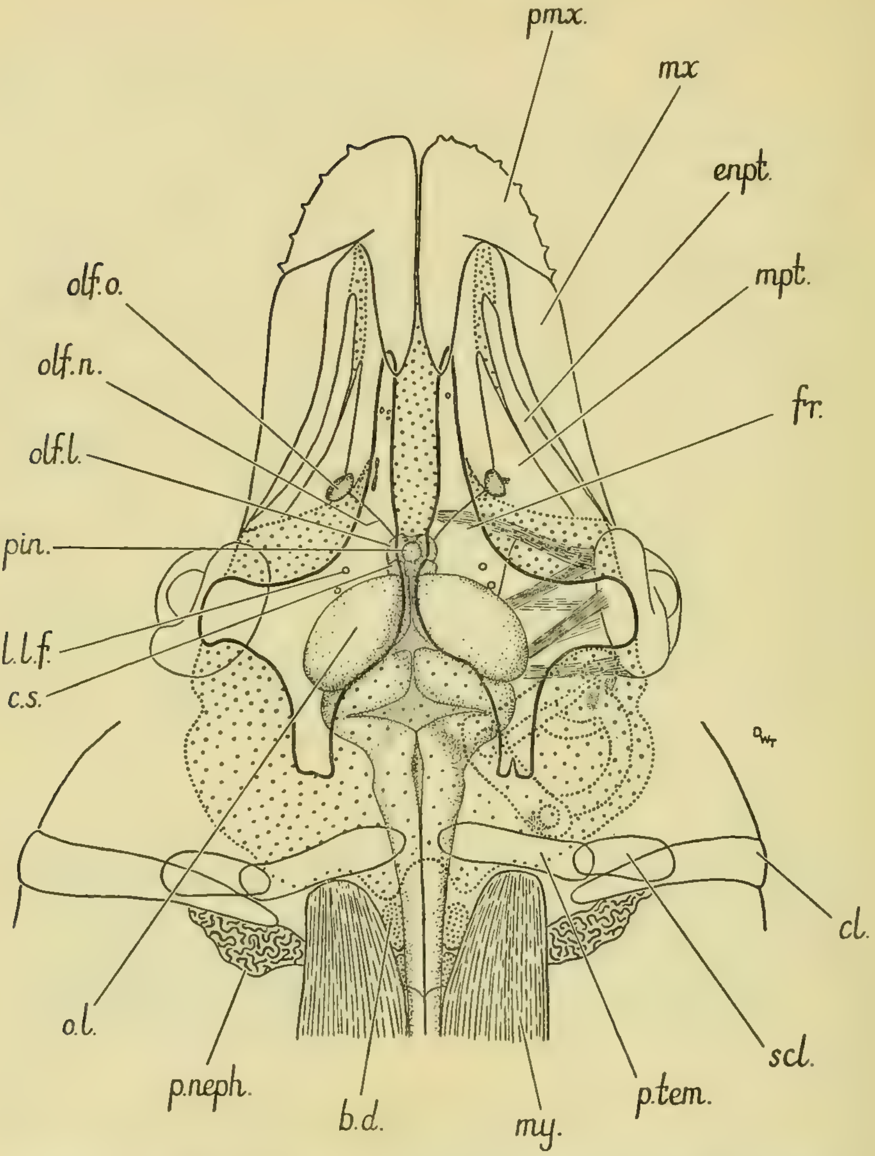
Visceral anatomy (Text-figs. 1 and 8)

The body-cavity is spacious and near-spherical.

The funnel-shaped pharynx narrows to a short oesophagus. The stomach is small with a median constriction. A single pyloric caecum bears subtle transverse surface undulations suggesting subdivision into three or four at a later stage. The intestine leaves the stomach to descend round the left side of the body, narrows as it runs transversely upon the lower body wall, ascends some distance up the right side, and then turns and runs obliquely downwards and backwards from right to centre to open on the anal papilla. There is some differentiation of texture and thickness in the regions of the gut, but no certain indication of a spiral valve nor of any rectal glands.

The pronephros was remarkably distinct even in the untreated material, a pear-shaped structure upon whose surface tubules are apparent, attached near the anterior somites and the upper end of the cleithrum.

The liver comprises two major lobes, narrowing as they run dorsally to left and right. A problematic strip of similar-seeming tissue may be pancreas; one cannot say.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Text-fig. 7. *Rosaura rotunda.* Dorsal anatomy of the head: the lateral scale slightly exaggerated due to drawing with a twin-objective microscope. Cartilage coarsely stippled. The eye-muscles and auditory organ of the left side are omitted to avoid over-complication. For key to abbreviations used see p. 181.

Of the heart may be seen a large spherical auricle, a smaller thick-walled ventricle, and a structure which must almost certainly be the sinu-auricular valve, though the sinus itself is too transparent to be distinguished. A large vessel runs in the mesentery to the middle of the intestine.

There is no trace of gonad development.

Musculature, etc.

The total number of myomeres developed is 37. Of these 16 are in front of the dorsal fin; the dorsal fin-base occupies 6½; there are 2½ between dorsal and adipose fins; the adipose fin-base occupies 3, and 9 remain to the end of the body. There are 22 myomeres before the anal fin, and the anal fin-base occupies 9½. The dorsal muscle somites are shallowest and forwardly extended where they are approximated to the posterior end of the cranium, and become progressively deeper towards the origin of the tail. The ventral body musculature forms a thin continuous balloon-like surface, much crinkled in preservation, and with only here and there a line to indicate a myocomma.

The *m. adductor mandibulae* has a superficial component inserted on the inside of the angular in advance of the jaw-articulation; another component inserted nearby on the maxillary, and a deep component which turns sharply forwards and inwards to an adjacent insertion on the inside of the dentary. The long tendon of the *m. adductor mandibulae* runs along the anterior edge of the hyomandibular-symplectic to an insertion on the head of the hyomandibular or somewhere on the skull close by.

A very strong ligament runs from the hindermost tip of the lower jaw along the hinder edge of the suspensorium to the region of the opercular. As in *Chauliodus* (Tchernavin, 1953, *The Feeding Mechanisms of a Deep-sea Fish* (B.M. [N.H.]), however, the opercular is small and the *m. levator operculi*, if present, consequently likely to be weak and relatively useless in opposition to the *m. adductor mandibulae*. I cannot see any ligamentous connection between the hind end of the mandible and the posterior end of the epihyal, and therefore assume that the main work of opening the jaws is accomplished by the *m. sterno-hyoideus*, which is well developed in common with the other muscles in the floor of the mouth.

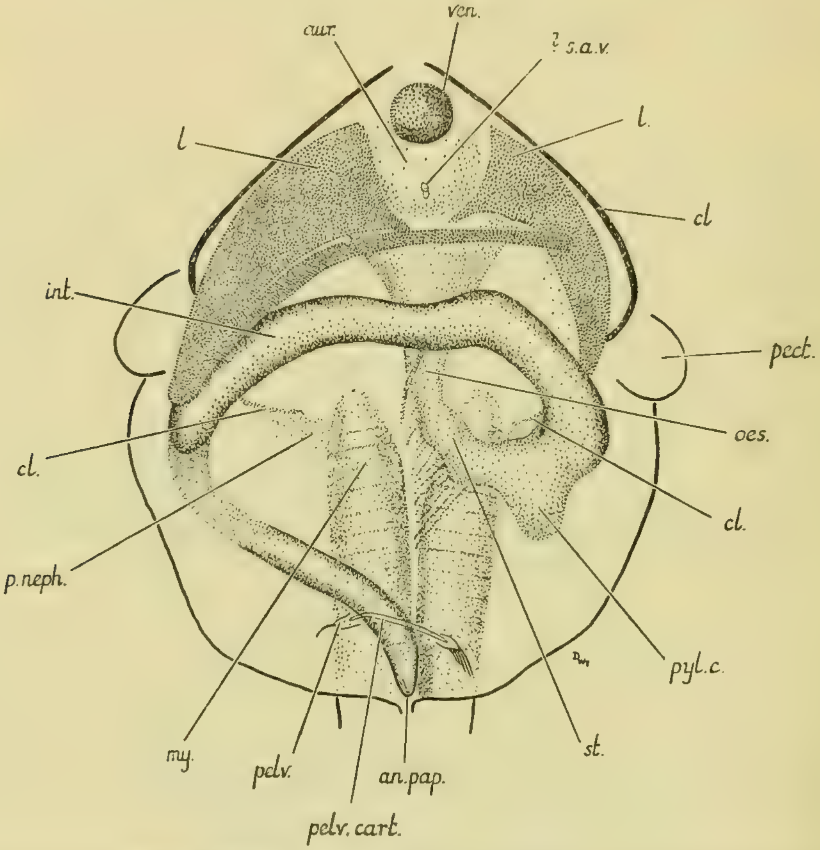
There is a patch of fibrous tissue binding the lower posterior end of the maxillary to the dentary.

The latero-ventral boundary of the buccal cavity is formed by a thin sheet of tissue, probably smooth muscle, whose lateral edge extends as an arc from the level of the middle of the symplectic to the tip of the basihyal.

The *abductor pinnae pectoralis* is a thick muscle between the coracoid cartilage and the anterior face of the pectoral fin; its strong development adds another obstruction to the observation of the radialia.

Traces of muscles are visible upon the hypurals of the caudal fan, together with a loose aggregation of myoblasts behind the ultimate somite.

The eye muscles are long and slender (Text-fig. 7). The *m.m. recti* and *m. obliquus* *inferior* require no special comment, but the *m. obliquus superior* is unusual in that it follows a very independent course to an insertion well forward on the ethmoid.



Text-fig. 8. *Rosaura rotunda.* Abdominal viscera, viewed from a point behind and below the vent. For key to abbreviations used see p. 181.

Nervous system and sense organs (Text-fig. 7)

Differentiation of the brain is well advanced, though there are no structures that call for very special notice. There are olfactory lobes with olfactory tracts running forward and outward through the ethmoid cartilage to the olfactory organs ; behind these lie corpora striata, and between them an epiphysis or pineal organ. The optic lobes are very large, as also is the cerebellum, and the third and fourth ventricles are readily distinguished. The swollen origin of the spinal cord is exposed between the anterior somites.

Key to abbreviations used in text-figures

ang,	angular.	*oes,*	oesophagus.
an.pap,	anal papilla.	*o.l,*	optic lobe.
aur	auricle.	*olf.l,*	olfactory lobe.
bas.h,	basihyal.	*olf.o,*	olfactory organ.
bd,	basidorsal.	*op,*	opercular.
brst,	branchiostegal ray.	*pect,*	pectoral fin.
cer.h,	ceratohyal.	*pelv,*	pelvic fin.
cl,	cleithrum.	*pelv.cart,*	pelvic cartilage.
cor,	coracoid cartilage.	*pin,*	pineal body.
c.s,	corpus striatum.	*pmx,*	premaxilla.
den,	dentary.	*p.neph,*	pronephros.
ecpt,	ectopterygoid.	*p.tem,*	post-temporal.
enpt,	endopterygoid.	*pyl.c,*	pyloric caecum.
eth,	ethmoid cartilage.	*q,*	quadrate.
fr,	frontal.	*r.a,*	retro-articular.
hm,	hyomandibular.	*? s.a.v,*	? sinu-auricular valve.
int,	intestine.	*s.cl,*	supra-cleithrum.
int.h,	interhyal.	*sym,*	symplectic.
l,	liver.	*s.op,*	sub-opercular.
l.l.f,	opening of lateral line canal.	*st,*	stomach.
mpt,	metapterygoid.	*ven,*	ventricle.
mx,	maxilla.	*vom,*	vomer.
my,	myomere.		

The eyes are laterally directed, set high on the head, and rather small for an oceanic fish. They are loosely suspended in orbits too big for them, but there is nothing else to evidence a post-*Stylophthalmus* condition. The line of suture of the choroidal fissure is quite distinct (Text-fig. 4).

The olfactory organs are minute and extremely difficult to interpret; they are undivided, and seem to have the structure of very shallow thick-walled funnels whose openings are occluded to elliptical chinks. There is a wisp of tissue depending from the edge of one which is of dubious significance.

The auditory labyrinth is very well developed; the three semicircular canals with their ampullae are present, and the cristae acousticae of the ampullae clearly visible (Text-fig. 7). Part of the otolith can be seen in the bulla in dorsal view, but its shape cannot be distinguished through the complicated light-refracting surfaces of the auditory capsule.

Very little of the lateralis system was visible in the untreated specimen, and that has since disappeared in clearing. There are pits with sense organs on the frontals (Text-fig. 7) and on the dentaries (Text-figs. 2 and 4), and one or two other organs of the suborbital and preopercular-mandibular series were faintly seen. There is no trace of a lateralis system on the body.

Portions of the IInd, IIIrd, IVth, VIth and VIIth cranial nerves have been noticed, but the observations were typical and too fragmentary to merit comment.

The surface of the body has many minute pilose projections. It is unlikely that these indicate anything more than muscle-fibre-bundles, but since damage to this specimen would have been of an all-or-nothing character, and in view of the discussion of lateral line papillae in other deep-sea fishes elsewhere in this paper, it may be worth while to put the observation on record.

Diagnosis and relationships of the Family Rosauridae

Isospondylous fishes in which the premaxillaries have long rostral processes; the maxillaries are toothless but enter into the gape; there are no supramaxillaries; the opercular apparatus is much reduced, the opercular being minute and the sub-opercular but slightly less so; the branchiostegal rays are long, slender and relatively numerous (10 in *Rosaura*) and support voluminous membranes; the eyes are laterally directed; the metapterygoid is large; an adipose fin is present; there is an unpaired pelvic cartilage (bone ?), and there is no post-cleithrum.

One known Genus *Rosaura* nov. with the characters of the Family, and with one species *R. rotunda* nov. based on a single immature specimen of 8·4 mm. S.L.

This definition is adequate to sustain the new family as distinct without involving characters likely to be modified in ontogeny. Additional characters present in the young *Rosaura rotunda* which will become significant if it can be shown that they are carried through to the adult stage are: the short, stout body; the non-telescopic eyes; the undivided nostrils; the absence of pre- and inter-opercular, pre-frontals and parietals.

In view of certain convergent similarities it may be as well to emphasize that the Rosauridae are readily removed from the Iniomi by their possession of premaxillaries which do not exclude the maxillaries from the gape; an unpaired ethmoid; an unforked post-temporal; and a reduced opercular apparatus.

Within the Isospondyli the affinities of *Rosaura* are difficult to trace, and it may indeed, like *Macristium*, represent one of those anomalous offshoots which are not likely to be related to any of the main branches. Perhaps its most likely relationship is to the Stomiatoids, which group have a moderate tendency towards the development of rostral processes, though less pronounced; a raptorial dentition (though usually with teeth on the maxillary, and supramaxillaries present); a tendency towards loss of the parietals and post-cleithrum, and a reduced opercular apparatus; and a high number of branchiostegal rays (19 in *Chauliodus*). The general body-form of *Rosaura* is not unlike that of the young stages of the Sternoptychidae. But none of these resemblances is very fundamental and the differences are formidable.

During a recent hurried visit Dr. Anton Fr. Bruun glanced at the specimen and drawings, and expressed the belief that he had seen this little fish in some numbers in the "Dana" Collections, and thought that a comparison with *Scopelengys tristis* Alcock might be worth making. I followed up his suggestion, but from a consultation of the literature and an examination of a specimen taken by the "John Murray" Expedition (Reg. No. 1939.5.24.463) find that the differences are very considerable.

Family SALMONIDAE

Salvelinus alpinus (Linnaeus)

Salmo alpinus Linnaeus, 1758, *Systema Naturae* : 309.
Salvelinus alpinus БЕРГ, 1932, РЫБЫ ПРЕСНЫХ ВОД СССР И СОПРЕДЕЛЬНЫХ СТРАН : 170 (*Berg, Les poissons des eaux douces de l'U.R.S.S.*, Leningrad. Text in Russian, full synonymy) ; Oliva, 1951, *Copeia* : 91, recent references).

St. 7. 9.ix.37. 60° 16′ N., 44° 41′ W. ; trammel net at mouth of stream entering Tasermuit Fjord, S. Greenland. (Pathological material.)

? Do. Three specimens, 222–330 mm. S.L. (No label.) Reg. No's. 1953. 3.6.8–10.

HAB. Arctic Boreal. (Anadromous and lacustrine races.)

If not collected on the same occasion as the pathological material, the entire fishes must certainly be from one of the S. Greenland stations. Concerning a tumour-bearing lower jaw J. S. Colman notes :

" When these tumours occur on the Char the fish are poor and thin and the Greenlanders will not eat them. The authorities at Julianehaab, S.W. Greenland, are very anxious to find out their nature and cause."

This specimen has been submitted to Prof. Alexander Haddow, Director of the Chester Beatty Research Institute, Royal Cancer Hospital, who forwards the following report by Dr. E. S. Horning :

" Microscopical Examination : Subcutaneous Fibroma.

> " Growth consists of fibroblasts and bundles of interlacing fibrous tissue, together with what appear to be, with this fixation," (Bouin) " elastic fibres. There is also a rather delicate stroma of connective tissue, in which run nutrient vessels lined by an irregular epithelium. This tumour has the appearance of a hard fibroma, as some areas show a tendency to undergo hyaline degeneration. It is definitely not a myxomatous type of growth, as there is no evidence of fatty degeneration."

Another case of tumours in *Salvelinus* has been described by Hoshina (*Jap. J. Ichthyol.* **2** (1952) : 81–88.

Family ALEPOCEPHALIDAE

(For a recent generic revision and summary of literature, see
Parr, 1951, *Amer. Mus. Novitates*, No. 1531 : 1–21.)

Leptoderma macrops Vaillant

(Text-figs. 9–13)

Leptoderma macrops Vaillant, 1888, *Poissons Expéd. Sci. " Travailleur " et " Talisman "* : 166, pl. 13, fig. 2 ; Goode & Bean, 1895, *Oceanic Ichthyology* : 49 (Washington) ; Koehler, 1896, *Rés. Camp. Sci. " Caudan "* : 523 ; Roule & Angel, 1933, *Rés. Camp. Sci. Monaco*, 86 : 8 ; Fowler, 1936, *Bull. Amer. Mus. nat. Hist.* **70** : 193 ; Bertin,[1] 1940, *Bull. Mus. Hist. nat. Paris* (2), **12** : 275 ; Rey, 1947, *Ictiologia Iberica*, **2** : 92 (Madrid) ; (?) Alcock, 1892, *Ann. Mag. nat. Hist.* (6) **10** : 361.

(?) *Leptoderma affinis* Alcock, 1899, *Cat. Deep-sea Fishes " Investigator "* : 182. Calcutta ; id., 1900, *Illust. Zool. " Investigator," Fishes* : pl. 32, fig. 3 ; id., 1902, *A Naturalist in Indian Seas* : 237, fig. 35 (London).

(?) *Leptoderma retropinna* Fowler, 1943, *Bull. U.S. Nat. Mus.* **100** Vol. 13, Pt. 2 : 55, fig. 5.

Leptoderma Springeri Mead & Böhlke, 1953, *Texas Journ. Sci.* **5**, No. 2 : 265 (received too late for inclusion).

St. 49. 1.ii.1938. 28° 25′ N., 13° 34′ W.; Agassiz trawl, *c.* 1,300(-0) metres. Three specimens, 85–150 mm. S.L. Reg. No's. 1953.3.6.5–7.

HAB. Deep Atlantic off N.W. Africa; Gulf of Mexico; Gulf of Gascony; ? Indian Ocean, Philippines. 650–2,300 metres.

The British Museum (Natural History) formerly possessed only a paratype (from the same station as the holotype, *fide* Prof. L. Bertin[1] *in litt.*) of this species, Reg. No. 1890.6.16.44, still bearing the usual Paris tie-on label punched 85 * 223. In all four specimens now available for study the delicate black skin has peeled forwards, leaving most of the body naked; as with Vaillant's other fifty-eight, therefore, "aucun des exemplaires n'est dans un état tout à fait satisfaisant." Koehler (1896) likewise complains: " . . . le tronc est complètement pelé." Roule & Angel (1933) fared no better: "Un exemplaire, en état défectueux . . . ."

The accounts of Goode & Bean (1895), Fowler (1936) and Rey (1947) appear to be dependent upon Vaillant's original description (1888); there is no evidence that these authors handled material themselves and all perpetuate Vaillant's errors. Koehler (1896) describes one specimen from the Gulf of Gascony. Roule & Angel (1933) merely add a locality record. Bertin (1940) lists Vaillant's material remaining in the Paris Museum as part of a general catalogue of types. Neglecting Alcock's very dubious specimen (1892, 1899, 1900, 1902) and Fowler's (1943) it appears that this species has been described only three times, and a new account may be of value.

GENERAL DESCRIPTION (BASED MAINLY ON THE LARGEST "ROSAURA" SPECIMEN)

Radial formula D.66; A.86; P.8; V.5–6; C.16.

Branchiostegal rays 6.

Gills 4 + pseudobranch.

Body naked, elongate, tapered, laterally compressed, especially in the long caudal region, where it becomes almost filiform (Text-fig. 9).

Head small, its length equal to the trunk and 5·55 in the length from tip of snout to caudal. Snout blunt, short, 1·27 times the interocular width and 1·40 in the diameter of the eye; it bears a short, blunt, laterally directed spinule on each

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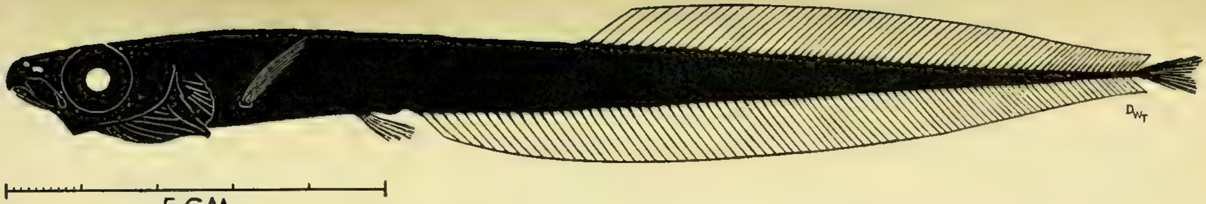
[1] Further consideration of Bertin's "Catalogue" reveals an unfortunate misapplication of the term "paratopotype," which affects not only the types of *Leptoderma macrops* but a great many others as well. Bertin states (*Bull. Mus. Hist. nat. Paris*, (2) **11**: 64, 1939):

> "Les autres sont des *paratypes* s'ils proviennent de la même localité que l'holotype ou des *paratopotypes* s'ils ont été pris dans d'autres régions."

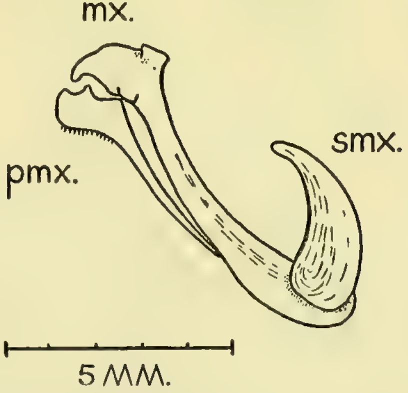
The term "paratype" need not necessarily imply any such geographic restriction, while "paratopotype" has hitherto denoted the exact opposite to Bertin's definition—c.f Alexander, 1916 (*Proc. Acad. nat. Sci. Philadelphia*, **68**: 496), who introduces the term earlier in the same paper and on the page cited defines it by implication; also Frizell, 1933 (*Amer. Midland Naturalist*, **14**: 659):

> "*Paratopotype*" (= paratype + topotype)—a paratype from the same locality as the holotype."

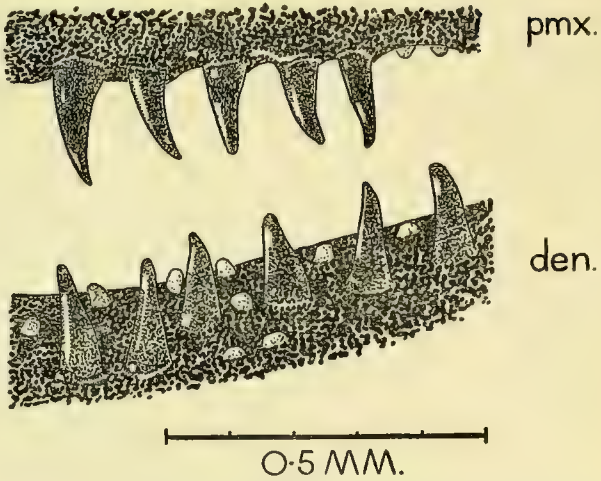
Bertin's two categories are already covered by the terms "*paratype omotype*" and "*paratype allotype*" proposed by Silvestri (in Holland, 1929, *Trans. 4th Inter. Congr. Entom. Ithaca*: 693); still-born expressions and unlamented by those who consider systematic zoology overburdened with redundant jargon. It is a pity that "paratopotype" is as well known as it is, for few users of Bertin's invaluable "Catalogue" will feel any need to refer back to his definitions and many will thus be misled.



TEXT-FIG. 9. *Leptoderma macrops.* Specimen of 150 mm. S.L. (Sensory papillae not shown). Text-figs. 10, 12 and 13 are taken from this specimen.



TEXT-FIG. 10. *Leptoderma macrops.* Bones of the upper jaw. *pmx,* premaxillary; *mx,* maxillary; *smx,* supramaxillary.



TEXT-FIG. 11. *Leptoderma macrops.* (Specimen of 130 mm. S.L.). Groups of teeth from the premaxillary and dentary, to the left of the symphysis in each case. The smaller, white structures are probably taste papillae.

side arising from the anterior end of the maxillary. Interocular space very slightly convex, almost flat, 1·79 in the diameter of the eye. Eyes enormous, projecting considerably on either side of the head, 2·78 in the head length. Nostrils large, their mid-point (in the shrunken condition of the specimen) approximately midway between the eye and the tip of the snout, the anterior smaller than and slightly dorsal to the posterior.

Mouth small, terminal to inferior. Upper jaw 1·20 times as long as the snout, barely reaching to anterior rim of orbit when the mouth is closed; lower jaw 1·36 times as long as snout, reaching to below anterior eyeball. Premaxillary slender, toothed, elongate, almost excluding maxillary from gape. Maxillary long, toothless,[1] curved, a small blunt spinule on its clubbed anterior end and a large -shaped supramaxillary at the posterior (Text-fig. 10). The space between the upper ends of the maxillary and supramaxillary is spanned by membrane, and the whole upper jaw well shielded in a sac of thin, tough skin forming a sound functional unit. The upper jaw rotates about its anterior end when the mouth opens and discloses a lightly pigmented recess on the cheek. The moving maxillary is steadied against a broad coronoid process of the dentary.

Teeth[1] in a single row in each jaw, about 14–20 on the premaxillary, seldom

TABLE I.—Leptoderma macrops: *Table of Measurements and Comparative Proportions*

It should be noted that Vaillant writes variously " Longueur " and " Longueur totale." In the present case he gives the length of the caudal fin as 3 (?) mm.; the likely error in a false assumption of standard length is therefore of the order of 0·1–0·4% underestimation in the figures quoted, and may be neglected.

	Rosaura specimen		Holotype
Total length	152 mm.		" Longueur 164 mm."
Standard length	150		
		Percentages of standard length	
Head length	27 mm.	18·0%	17·6%
Tip of snout to pectoral fin	32	21·3%	—
,, ,, pelvic ,,	49	32·6%	—
,, ,, vent	55	36·6%	*ca.* 37·5% (3/8)
,, ,, anal fin	57	38·0%	—
,, ,, dorsal fin	75	50·0%	—
Greatest depth of head	12·4	8·2%	—
,, ,, body behind head	11	7·3%	6·7%
,, thickness of body behind head	8	5·3%	4·2%
Depth at vent	9·7	6·4%	—
Length of pectoral fin	12·2	8·1%	—
Longest ray of dorsal fin	8	—	—
,, ,, anal ,,	9	—	—
Least depth of caudal peduncle	0·7	0·4%	—
		Percentages of head length	
Snout	6·9 mm.	25·5%	27·5%
Eye	9·7	35·9%	37·9%
Interorbital width	2·4	8·8%	17·2%
Interocular ,,	5·4	20·0%	?
Upper jaw	8·3	30·7%	—
Lower ,,	9·4	34·8%	—
Greatest depth of head	12·4	45·9%	—
,, breadth ,, (across eyes)	14·6	54·0%	—

---

[1] I am unable to find the "single row of minute conical teeth" at the anterior end of the maxillary, described by Mead & Böhlke (1953). But theirs is a larger specimen (190 : 150 mm.).

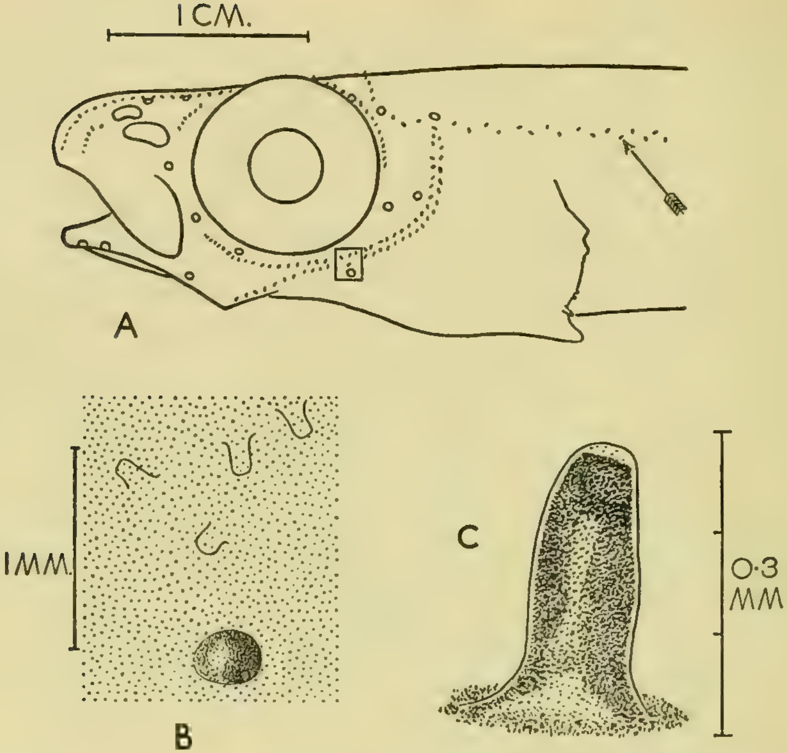
extending far to the side, and about 12–15 on the dentary. The teeth in each jaw are simple, slightly incurved, readily depressible fanglets (Text-fig. 11), and do not exceed 0·2 mm. in length in the largest specimen available. There is a danger of being misled into believing that the dentition is multiseriate, because rows of white structures (believed to be taste-buds rather than photophores) stand immediately behind the teeth, as well as being lavishly scattered over the lips (Text-fig. 11), and buccal cavity. The teeth may be largely concealed behind the lips; this condition varies in different specimens. There seem to be no palatine or vomerine teeth.

Gill-opening wide, though only extending upward to the level of the middle of the eye; membranes voluminous, posteriorly separate and free from the isthmus. The six branchiostegal rays and the opercular bones which together form the gill-cover are all concealed under heavily-pigmented skin, so that only the more prominent ridges of the bones show white at the surface and their boundaries are largely concealed. The preopercular has a long elbowed ridge extending from a point midway between the eye and the top of the gill-opening to the articulation of the jaw. The interopercular accounts for another ridge arising in the angle between pre- and sub-opercular and running some way with the former. The opercular has about a dozen ridges, some of which terminate in small denticulations at the hinder margin. The subopercular has one principal ridge which supports a small lobe at the lower posterior corner. The branchiostegal rays are slender and increase in length posteriorly; the sixth appears (without dissection) to be a rather stouter structure of T-shaped cross section (Hubbs' "branchioperculum").

Gills 4; a pseudobranch of half-a-dozen filaments present on the inside of the gill-cover. Gill-rakers 12 on lower limb of first arch; lanceolate with a few minute bristles. Gill-filaments rather short, leaf-like, shorter than rakers.

Pores of lateralis system of head few and large; 3 in the supra-temporal series, 3 or more in the supra-orbital, 4 in the infra-orbital, 5 in the preoperculo-mandibular (Text-fig. 12A). There may be others on the snout.

The thin skin of the body has been stripped forward and hangs in tatters about the head; it is possible, however, to paint a few centimetres of it back into position with a fine brush, and to decide pretty certainly that there were no lateral line pores on the body. Except that the skin tends to fold into a groove of uncertain significance neither is there any sign of a lateral-line canal upon the skin, nor upon the horizontal septum of the body. There are, however, upon the head and along the skin of the body large numbers of "tag organs" or lateral line papillae, in tracts corresponding to the theoretical lateralis distribution although quite possibly independently innervated (Text-fig. 12A, B). These papillae are compressed, closed, and of much the same shape and variability of form as the common littoral sponge *Grantia compressa*. The papillae of the body (Text-fig. 12C) and operculum are longest, and approach 0·3 mm.; they are heavily pigmented save at the tip and in a very narrow marginal zone, and have a core of connective tissue which is in some cases seen to be penetrated by a short branch of a nerve running along the papilla-tract. It is presumed that sensory cells were located in the tips of the papilla, but surface magnification reveals none, and since the fishes have taken a



Text-fig. 12. *Leptoderma macrops.* A. Diagram showing disposition of lateral line pores and sensory papillae over the head and trunk. B. Three papillae of the suborbital series, and a papilla and a pore of the preoperculo-mandibular series. (The area enclosed in the square on A, more highly magnified.) C. A single sensory papilla from the body. (That arrowed in A, more highly magnified).

great deal of punishment in the trawl the chances of their preservation are considered too slight to justify sectioning for the present.

Upon the head the papillae become shorter and squarer, until on the tip of the snout and about the lips they become very small, lose their pigment, and become superficially identical with the presumed taste-organs inside the mouth. (See further discussion on p. 193.)

The vent opens on a slight prominence exactly three-eighths the standard length from the tip of the snout.

Pectoral fins long, narrow, obliquely inserted about one-fifth the body-height from the ventral surface. All the rays except one are deeply forked, nearly to their bases.

Pelvics ventral, abdominal, separated by the width of one base, reaching to the anal.

Dorsal and anal fins very long, extending almost to the caudal, and each erected fin much taller than the body depth at the same level. The anal commences immediately behind the vent ; the dorsal much further back at the level of the 15th anal ray.

Caudal with a distinct and very slender peduncle, ending in a rather prominent little fan-like expansion of hypurals. The caudal rays are much damaged, and both the length and the count likely to be underestimated.

Colour (in spirit) deep purple-black all over the body, inside the buccal cavity and gill-chamber (and probably inside the body-cavity) ; considerably lighter on the snout tip and eyeballs. There is no evidence of organized photophores, though this does not preclude general luminescence of the epidermal mucus.

The largest specimen to hand is a female, with opaque white eggs of varying diameters (0·4–1·2 mm.) extruding from the vent. The extrusion is probably a decompression phenomenon, although Vaillant has already commented upon the great variation in the sizes of the eggs in this species.

COMPARISON WITH VAILLANT'S DESCRIPTION (1888)

Vaillant's description is comprehensive, detailed, and for the most part more accurate than most work of his period. Despite the few marked discrepancies now to be noticed there could be no reasonable doubt but that the present material should be referred to Vaillant's *L. macrops*, even without the advantage of a paratype for comparison. The new account is more an expansion of Vaillant's than a correction, although paucity of material leaves his account of the internal anatomy unchecked.

Vaillant gives D.48, A.71 +, and his figure agrees, showing these fins extending nearly to the caudal. The paratype now to hand, a specimen of 123 mm. S.L., gives practically these counts in median fins ending abruptly more than a centimetre *before* the caudal, and beyond their terminations there remains little more than vertebral column and a few tattered caudal rays. Having regard to the spacing of the posterior rays, and assuming that the fins once reached nearly to the caudal, as they do in Vaillant's figure and in the " Rosaura " material (which, it must be noted, was collected not far from the type-locality and at a similar depth), I estimate D.46 + *ca.* 20, A.74 + *ca.* 12, a precise correspondence with the " Rosaura " specimens. It is possible that Vaillant's artist reconstructed the dorsal, anal and caudal in their correct relations, perhaps from a better specimen, and fitted in the rays in accordance with counts supplied by Vaillant himself from a different fish.

Later in his text Vaillant gives P.15 (uncountable from the figure). Though at first I agreed, counting from the projection of the fin through a hole in the loose skin, I later found that I had merely repeated his error in counting the branches of rays which bifurcate close to their bases. Of the ventrals Vaillant remarks only that they are " si rapprochées qu'elles semblent se confondre " ; the figure appears to show V.5 or 6 and I count V.5 on the specimen.

The measurements available and shown in the comparative table (p. 186) show close agreement, except at one point where it seems evident that Vaillant's " interorbital " corresponds with my " interocular." He gives B.V + instead of B.VI ; he slightly undervalues the length of the maxillary ; he mentions the dorsal fin originating over the 23rd anal ray instead of the 15th—a likely variation and one common in other elongated fishes, such as *Notacanthus* for example ; and he fails to notice the sensory papillae, which, with the condition of his material and the probable magnification used in examining his specimens, is understandable enough. (Vaillant seems to have been impressed by the minuteness of the teeth—" assez peu developpées, pour n'être visibles qu'à un assez fort grossissement "—and the papillae of the lips and snout are smaller still, while, having decided that the lateral line was absent, Vaillant might well have felt no need to examine the skin of the body.)

COMPARISON WITH *LEPTODERMA AFFINIS* ALCOCK, 1899

Alcock (1892) described as *L. macrops* a single fish of 8¾ inches (222 mm.) S.L., trawled by the " Investigator " at 753 fathoms (1,357 metres) in the Bay of Bengal ; later (1899, 1900, 1902) he published a fuller description and figured it as *L. affinis*. Mr. A. E. Parr (Director of the American Museum of Natural History, at present engaged on a monograph of the Alepocephalidae) tells me that on inquiry of the Indian Museum, Calcutta, recently he learned that Alcock's unique holotype had been lost. No other records of Indian Ocean material have been given and Alcock's papers therefore provide the only evidence for consideration.

The invariably damaged condition of *L. macrops* in collections has been emphasized ; *L. affinis* stands in striking contrast, although the conditions of its capture were not particularly auspicious. Alcock makes no mention of the skin peeling from the body and is able to describe the lateral line in its entirety ; thus (1899) :

> " . . . a row of pores extends from the occiput to the caudal. In spirit the colour is purple, the contracted opaline epidermis forming a sort of bloom."

Again, the popular account (1902) :

> " . . . it is quite black and has no special phosphorescent glands, yet its entire skin is enveloped in a thick, opalescent epidermis, like a luminous ' bloom.' The only specimen captured glimmered like a ghost as it lay dead at the bottom of a pail of turbid seawater."

We can be satisfied as to the perfect condition of Alcock's specimen, and wonder indeed whether its apparent resistance to abrasion in the trawl may not indicate a specific difference from the Atlantic form. Alcock (1899) concludes :

> " This species seems to differ from *Leptoderma macrops* Vaillant in having the body less elongate, the lateral line very distinct, and the rays of the dorsal and anal fins more numerous. It agrees fairly well with the figure but not with the description of that species, and is probably identical with it."

The revised fin-ray counts for *L. macrops* show a remarkable similarity to those for *L. affinis*. Adding pectoral and caudal counts taken from Alcock's figure (1900) to the incomplete formula published in 1899, we have :

L. affinis D.*ca.* 66 ; A.*ca.* 85 ; P.8 ; V.5 ; C.17
L. macrops D.66 ; A.86 ; P.8 ; V.5–6 ; C.16

Despite this similarity there remain several serious discrepancies between the two species.

(1) *Body proportions.*—From Alcock's publications it may be deduced that in *L. affinis* the body-height measures 12·6% and the head-length 25·7% in a standard length of 222 mm. (Alcock does not state whether " standard " or " total " length is intended in this case, but his frequent mention of " length without caudal " elsewhere in his report of 1899 sufficiently indicates his custom. The proportions given, being taken from his figure, are unaffected by this consideration). Comparative figures are 6·7%, 17·6%, 164 mm. for Vaillant's holotype, and 7·3%, 18%, 150 mm. for the largest " Rosaura " specimen of *L. macrops*.

It would be hard to attribute these wide differences to the effects of ontogenetic changes, geographic variation and the fortunes of preservation. There is in fact evidence that the relative size of the head decreases with age in *L. macrops*, whereas the identification of *L. affinis* with *L. macrops* would require a contrary tendency.

	L. macrops					*L. affinis*
	" Rosaura "	Paratype	" Rosaura "		Holotype	(Alcock)
Standard length (mm.)	85	123	130	150	164	222
Head as % S.L.	20·5	19·5	18·4	18·0	17·6	25·7

One further explanation may be considered. The caudal peduncle in Alcock's figure is short and deep ; despite the disarming elegance of the caudal fork is it possible that the figure represents a truncated and regenerated tail ? If so, then estimates of the length of the missing portion based on computations of the length necessary to reconcile the proportions of *L. affinis* with those of *L. macrops* should show reasonable agreement.

	L. macrops	*L. affinis*	Estimated truncation.
Standard length	150 mm.	222 mm.	—
Head length	18·0%	57 ,,	94 mm.
Snout to anal	38·0%	105 ,,	65 ,,
Snout to dorsal	50·0%	129 ,,	36 ,,

This hypothesis is clearly untenable also.

(2) *Lateral line.*—Alcock comments upon the apparent difference between his species and Vaillant's in this respect ; it was a point which he would undoubtedly have verified. I have examined the skin and bodies of four specimens of *L. macrops* and find no pores save on the head ; it seems hardly likely that the stripping of the skin should destroy them so thoroughly as to defy microscopic examination. Yet is Alcock truly representing the case when he speaks of " a line of pores " ? His figure suggests, rather, a line of sense organs lying flush with the skin.

(3) *Sensory papillae.*—Nineteenth-century workers[1] did not often use very high magnifications when examining fishes, and Alcock may have overlooked papillae for this reason, as did Vaillant.

(4) *Supramaxillary.*—I find one supramaxillary in *L. macrops*, as also did Vaillant —" un sus-maxillaire distinct," " un petit osselet en serpe." Alcock (1899) on the other hand speaks of a maxilla which " is very broad and consists of three pieces." It is unthinkable that he should have included the entire premaxillary in this trio, but very likely, as his figure seems to indicate, that he mistakenly dissociated the posterior process of the premaxillary from that bone as a second supramaxillary.

(5) *Pectoral fin.*—The pectoral of *L. macrops* is low on the body and almost horizontally inserted. Alcock's figure shows that of *L. affinis* much higher and practically vertically inserted.

The evidence seems at the very least to support the retention of *Leptoderma affinis* Alcock as a distinct species. If Alcock reported correctly the presence of *two* supramaxillaries, moreover, we are faced with a distinction of generic importance, and one which Parr (1951) uses as the basis of the first dichotomy of his key to the genera of Alepocephalidae. Conversely, with the retention of *L. affinis* in *Leptoderma*, the key drafted by Parr will require modification of the stated body-proportions, as well as of the fin-ray counts corrected by the present work.

BIONOMICS AND ADAPTATIONS OF *LEPTODERMA MACROPS*

> " . . . the 'Michael Sars' at Station 48, between the Canaries and the Azores, brought up an *Alepocephalus* in the large trawl towed at the bottom in 5,000 metres, just as these fishes have been captured by most deep sea expeditions ; on the trawl-rope a small tow-net was fixed in such a way that it was towed about 1,000 metres above the bottom and in this net an *Alepocephalus* was also captured. Such facts warn us against hasty conclusions.
>
> MURRAY & HJORT, 1912, *The Depths of the Ocean* : 412. London.

Leptoderma macrops has (on published records) been taken in ten trawl hauls ; by the " Talisman " (6), " Caudan " (1), " Princesse Alice II " (1), " Oregon " (1), and now the " Rosaura " (1), in depths ranging from 650–2,330 metres. Of a total of 65 specimens 59 were collected by the " Talisman ", 47 at St. 93 on the Banc d'Arguin. This paucity of records is remarkable when one considers the number of bottom hauls made by, say, the " Michael Sars," within the known range of the species and without results. Unless the " Talisman " encountered a breeding concentration the fish seems singularly capricious in its occurrence.

The association of predominantly bottom fauna with *L. macrops* is indicated in the reports of Vaillant (1888) and of Roule & Angel (1933). At " Rosaura " St. 49 it was accompanied by 2 *Bathypterois dubius* Vaillant (with minute eyes and tactile pectorals) ; 5 *Gadomus longifilis* (G. & B.), 1 *Gadomus arcuatus* (G. & B.), 5 *Bathygadus vaillanti* Roule & Angel, 1 *Halosaurus oweni* Johnson, 1 *H. johnsonianus* Vaillant and 29 *Synaphobranchus pinnatus* Gronov. In anticipation of the invertebrate papers, and by courtesy of Dr. M. Burton, Mr. N. Tebble, Dr. I. Gordon,

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[1] Charles Darwin, for example, had a great preference for the simple microscope, and had no compound microscope with him on his " Beagle " voyage (*Life and Letters*, ed. F. Darwin, **1** : 145. London, 1888).

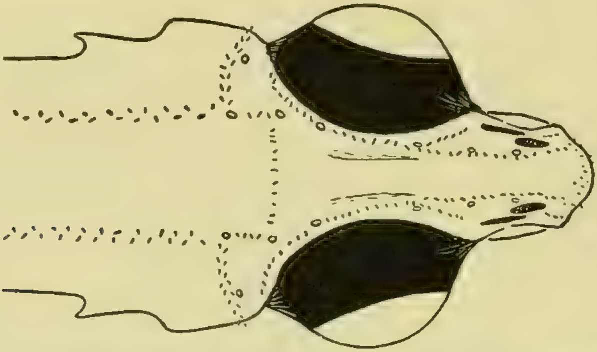
Dr. W. J. Rees and Miss A. M. Clark, it is possible to report associated bottom fauna in the groups Porifera, Polychaeta, Decapoda, Mollusca (dead pteropod shells) and Echinodermata. Preliminary assessments indicate that no mid-water species were taken in any group.

All the available evidence therefore points to *Leptoderma macrops* being a fish living on the bottom beyond the Continental Shelf. That it is of the select group of deep-sea fishes which perform considerable vertical migrations is unproven and unlikely : its general appearance makes this seem much more improbable than in the case of *Alepocephalus macrolepus* Koefoed (1910, *Sci. Rep. "Michael Sars,"* **4** : 44), the fish whose exploit is recorded in the cautionary text at the head of this section.

Little can be learned from the gill-rakers. The filaments suggest that cutaneous respiration has permitted a reduction in their size. The small gape, puny dentition and unathletic form point to a fish living upon detritus and/or small and feeble prey. The jaws are not protractile, though the maxillaries are practically vertical when the mouth is fully opened, so that in one way the following comparison is invalid, but the great number of taste-organs in the mouth may point to the fish living like a deep-sea carp, sucking-detritus from the bottom and sampling it for nutritious particles. (I have not gutted the specimens, for obvious reasons, but a radiograph of the largest shows objects in the stomach which resemble a small lamellibranch shell and a couple of large sponge spicules.) The system of lateral line papillae, obviously useful in warning of enemies, may be used offensively against small prey such as polychaetes and crustaceans, a vibration in the water being followed by a reflex snap and a leisurely assessment of the catch by the taste organs. (See also p. 194*ff*.) In either case Walls' dictum holds : "Go far enough along the bottom (if you're a fish), and you're bound to bump into something good to eat."

The excellent summary of the eyes of deep-sea fishes by Walls (1942, "The Vertebrate Eye," *Bull. Cranbrook Inst. Sci.* **19** : 391–405) is the starting point for the discussion which follows. Vaillant (1888) has admitted that his published figures do not adequately represent the lateral protrusion of the eyes of *Leptoderma*. The diagrammatic reconstruction presented in Text-fig. 13 attempts to do this, and, it is believed, with considerable accuracy. The largest "Rosaura" specimen was used for it, the left eye being undamaged, and in an apparently normal position in the orbit, and the shrunken cornea was gently pulled out to its proper convexity with fine forceps. The lens is not shown ; in dorsal view it is concealed under the pigmented portion of the eyeball, and whether this condition is normal or not it is certainly very large, much larger than the diameter of the pupil.

These eyes are enlarged, but quite unlike those of the fishes of the twilight zone, such as *Epigonus* and *Aphanopus*. If Walls is correct in stating that the eyes of *Bathytroctes* and *Platytroctes* are "apparently in a half-way stage of evolution toward an eventual forward-aimed, tubular organ" like those of *Gigantura* and *Winteria*, then it must be admitted that *Leptoderma* is a great deal more advanced towards the same type. The parallel tubular eyes already cited are, like the upwardly directed ones of *Argyropelecus* and *Opisthoproctus*, most likely concerned with space-perception, assessing the distance of the infrequent flashes from the photophores of other organisms. With a light penetration limited to 400 metres depth it is most unlikely that *Leptoderma* can ever aspire even to the twilight zone; the structure of its eyes makes it seem most unlikely that it can form a distinct image under whatsoever lighting conditions, and yet it is clear from Text-fig. 13 that if light-sensitivity be admitted as "vision" *Leptoderma* has, by moderate nasad asymmetry and considerable protuberance of the eyes, achieved a very fair degree of stereoscopic vision, if not of binocularity. If its eyes have largely lost their effectiveness as cameras through structural modification and conditions of intense darkness (and it will be noted that the small ocular photophores concerned with neuro-facilitation in fishes which rely on normal vision below the photic zone are not developed in this genus), it is still obvious that they have a high degree of potential usefulness as range-finder photometers, capable of locating animal and bacterial luminescence and enabling assessment of its potentialities as food or foe.



Text-fig. 13. *Leptoderma macrops.* Diagrammatic reconstruction of dorsal surface of head, showing lateral projection of the eyes.

The associated bottom fauna from St. 49 included numerous specimens of *Polycheles* spp. and *Heterocarpus* sp., crustacean genera whose Indian Ocean species at least are known to be luminous, and also the Asteroid *Brisingella coronata* which belongs to a family whose luminescence is in dispute. It is also interesting to note that in this one haul the enlarged eyes of *Leptoderma macrops* are paralleled in a polychaete *Robertianella* and a crustacean *Heterocarpus*, while the reduced eyes of *Bathypterois dubius* are parallelled in the crustacea *Nephropsis atlantica* and *Polycheles* spp.

OCCURRENCE AND SIGNIFICANCE OF SENSORY PAPILLAE IN DEEP-SEA FISHES

Papilliform lateral line organs have been reported in several quite unrelated groups of deep-sea fishes. Zugmayer (1911, *Résult. Camp. Sci. Monaco*, **35**: 92, pl. iv, fig. 3) records them among the Lyomeri in *Gastrostomus* (= *Eurypharynx*). Pfüller (1914, *Z. Naturw. Jena*, **52**: 1) in an intensive study of the lateral line organs of the Macruridae gives accounts and figures sections of papillae in *Coelorhynchus* and *Macrurus*. Roule & Bertin (1929, *Dana Reps*. No. 4 : 12) mention the co-existence of lateral line pores and papillae in the deep-sea eel *Nemichthys*, and the same authors (op. cit. : 53) and Trewavas (1933, *Proc. zool. Soc. London* : 601) describe a variant of the same condition in the nearly-related *Cyema*. The most comprehensive demonstration of papilla variation is given by Regan & Trewavas (1932, *Dana Reps*. No. 2 : 23), who describe and figure five distinct types in the Ceratioid Angler-fishes, and show that the several families may be classified into five corresponding groups. Their *Dolopichthys* papilla approaches most nearly to that of *Leptoderma*.

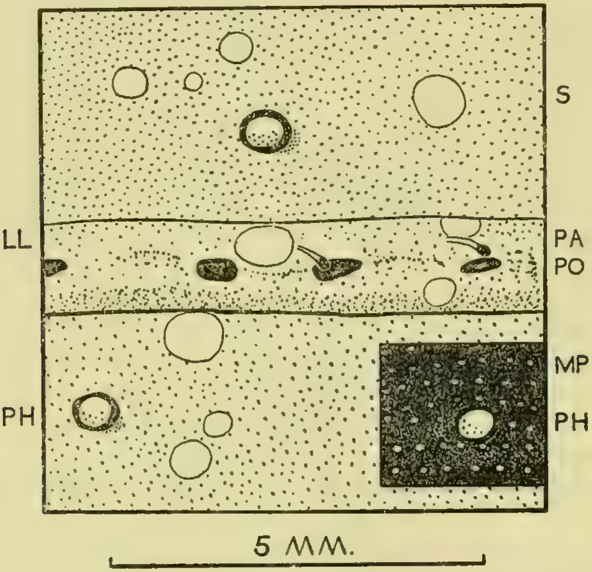
Among the Alepocephalidae, however, no very precise demonstration seems to have been given before the present. In the Alepocephalidae *sensu lato* (including Parr's Searsidae), Brauer (1906, *Wiss. Ergeb. Deutsch. Tiefsee-Exped. " Valdivia,"* **15** : 17 *et seq*.) describes " papillen " in several species, with recognizable figures, but makes no functional distinction between photophores general and special, the " shoulder organs " of Searsidae, and true lateral line papillae. The species mentioned by Brauer, in none of which seems a *Leptoderma* condition to be clearly demonstrated, are :

Fam. Alepocephalidae
Bathytroctes longifilis (= *Nemabathytroctes longifilis* (Brauer)).
Aleposomus lividus (= *Rouleina lividus* (Brauer)).
Aleposomus nudus (= *Rouleina nudus* (Brauer)).

Fam. Searsidae
Bathytroctes rostratus (*nec* Günther) (= *Searsia koefoedi* Parr).

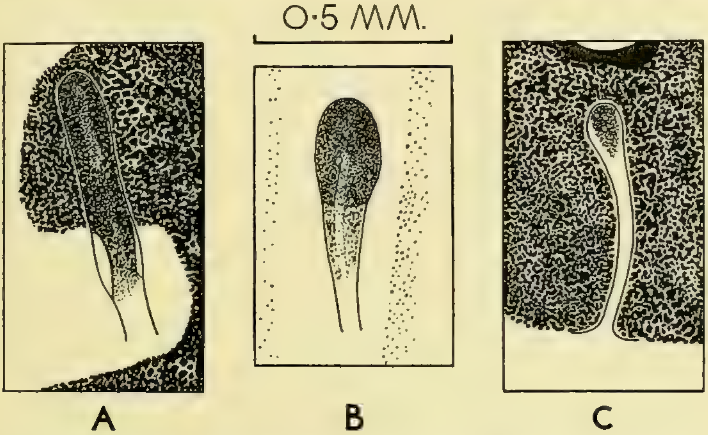
Beebe (1933, *Zoologica, N.Y.* **16** : 17) describes a pattern of tubercles in his *Anomalopterus megalops*, but which can hardly be reconciled with a lateralis distribution (nor, for that matter, Beebe's species with *Anomalopterus* Vaillant (now *Anomalopterichthys* Whitley, the name being several times preoccupied). Beebe (op. cit. : 83) also describes small stalked structures in *Photostylus* which he regards as photophores, but which may well be primarily sensory papillae ; these also are not regularly arranged.

Unfortunately many genera of Alepocephalidae are not yet represented in the collections of the British Museum (Natural History) but a rapid search for other forms bearing lateral line papillae has been rewarded. The holotype of *Xenodermichthys nodulosus* Günther (1887, *Sci. Rep. " Challenger " Zool*. **22** : 230, pl. 58, fig. c) is much as Günther described it, with a normal tubular lateral line, and a tough skin scattered with minute white scale-like structures and small, nodular and undoubted photophores. Somewhat surprisingly Günther failed to notice that almost the whole of the head (including the isthmus) is unpigmented (save for the photophore rims), intact, and sharply distinguished from the body ; a few years later and he must surely have noted an appearance strongly recalling the all-luminous head of *Aulastomatomorpha*. He also missed the lateral line papillae : minute, club-shaped, with slender colourless attachments and black tips (Text-figs. 14 and 15). They are arranged in single and double linear tracts upon the head, corresponding to the *lateralis* distribution, and are upon the body rather sparsely placed immediately above the lateral line tube and upon the tube itself, either between or above the lateral line pores. Down the upper limit of the gill-cover, along the boundary between pigmented and unpigmented integument, the papillae are more elongate and their stalks whiter; they resemble photographic negatives of the fungus *Xylaria hypoxylon*. Von Lendenfeld (1887, "*Challenger*" *Reps. Zool.* **22**, Appendix B.: 307, pl. 53, figs. 49–53) has described the histology of the photophores and mucus glands, but again does not mention sensory papillae. It is likely that he was given a piece of tissue from the flank (missing in the specimen) which would not have borne any papillae, and that he did not receive the entire fish for examination. Rauther (1927, *Bronns Tierreich*, **6**, Abt. 1, Book 2: 125) in his discussion of light organs in fishes regards the first-mentioned structures as sensory organs.



TEXT-FIG. 14. *Xenodermichthys nodulosus* Günther. (Holotype, 180 mm. S.L.). Portion of skin from the left flank. The lateral line, LL, crosses the centre of the figure. PO, lateral line pore; PA, papillae; S, rudimentary scale, three of which may be seen supporting the outer wall of the lateral line canal from within; PH, large photophores, arranged in alternating segmental rows so as to mark out rhomboidal areas on the body; MP, very numerous white spots, possibly luminous (mucus glands according to von Lendenfeld), arranged in close longitudinal rows.

Convergent evolution of lateral line papillae in several widely separated groups of deep-sea fishes has not yet received an explanation, despite its clear adaptive value. All the fishes concerned are forms of inconsiderable locomotive powers, not subject to violent water movements consequent upon their own swimming, and living at depths beyond the range of wave action and of strong currents. In such conditions extreme exposure of lateral line sense organs upon papillae results in no redundant irritation to the fish; on the contrary, it must materially assist the apprehension of the slightest local disturbance in the water, and be a vital asset in the collection of information from an environment that can impart so little so reluctantly to the more orthodox sense organs. It is probable that the lateralis system in these fishes allows precise location and capture of small prey without any visual assistance. Experimental evidence in support of this theory may be derived from the experiments of Dykgraaf (1932, *Z. vergl. Physiol.* **17** : 802), who showed that the freshwater minnow *Phoxinus* can be trained to snap at small bodies gently agitated in the vicinity of its caudal lateral line papillae; in this case, however, the sensory cells are situated at the bases of the tubular papillae, instead of at the tips as in the deep-sea fishes so far investigated. For a general introduction to this subject see Pfüller (*ante*) and Wunder, 1936 (in Demoll & Maier, *Handbuch der Binnenfischerei Mitteleuropas*, 2B : 49. Stuttgart).



TEXT-FIG. 15. *Xenodermichthys nodulosus.* Three types of sensory papillae. A. Stout papilla from occipital region, at the boundary between pigmented and unpigmented integument. The papilla bears two large photophores towards its base, and has a number of minute, intense white spots scattered over its surface, probably further photophores. B. Clavate papilla standing upon the supra-orbital canal. The papilla is traversed by a nerve, and has presumed minute photophores over its surface. This is a type which punctuates rows of similar papillae of about half the height in the lateralis system of the head. A similar size and type of papilla to this stands upon and above the lateral line canal of the body. C. Slender-stalked papilla, type confined to upper margin of operculum, along boundary between pigmented and unpigmented integument. (Text-figs. A, B and C are drawn to the same scale.)

Family SEARSIDAE.

Parr, 1951, *American Museum Novitates*, No. 1531 : 1–21.

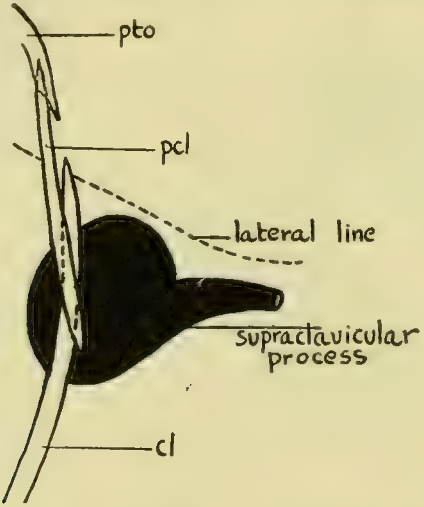
ALEPOCEPHALIDAE (part)

Günther, 1887, "*Challenger*" *Reps. Zool.* **22** : 227–8.
Brauer, 1906, *Wiss. Ergeb. deutsch. Tiefsee-Exped.* "*Valdivia*," **15** : 17–18.
Beebe, 1933, *Zoologica N.Y.* **16** : 36–56.
Parr, 1937, *Bull. Bingham Oceanogr. Coll.* **3** : 12–19.
And numerous other authors.

NOTES ON TAXONOMIC AND STRUCTURAL FEATURES

(1) *Shoulder organ*

The Searsidae have been separated off from the Alepocephalidae by Parr (1951), and are characterized by the possession of a peculiar structure which Parr, in this, his latest paper, calls the "shoulder organ," which name is the least unsuitable of those so far applied. The new family forms a quite distinct group, and its recognition seems surprisingly overdue, although one regrets its immediate proliferation of new subfamilies, genera, and subgenera.



Text-fig. 16. Diagram of shoulder organ ("supraclavicular process") in a young Searsid, showing its relation to pectoral girdle and lateral line. *pto*, post-temporal; *pcl*, supracleithrum; *cl*, cleithrum. (From Beebe, 1933.)

The shoulder organ, *alias* "supraclavicular organ/process" and "postclavicular organ," lies neither upon nor behind the shoulder-girdle, but within it (Text-fig. 16).

Overlooked by nineteenth century authors and their artists (as well as several later ones) it seems first to have been noted by Brauer (1906) :

> " Dorsal von der Brustflosse liegt eine grössere nach hinten gerichtete Papille."

Beebe (1933) notes its gross structure, provides the figure here copied, and mentions ontogenetic changes :

> " In cleared specimens the supraclavicular process is seen to be a retort-shaped sac, with a posteriorly directed neck terminating in a single pore. This seems to be the only opening, external or internal, to the organ, which arises just interior to the pectoral girdle at the junction of the supracleithrum and cleithrum, well below the lateral line. The posterior part of the sac and the entire neck are exterior to the body wall. It is possible that, instead of being greatly reduced in relative size in larger specimens, as is generally believed, the organ merely has a smaller part of its surface projecting exteriorly."

To this account I can add that in the smaller " Rosaura " specimen now available (Text-fig. 17) there is evident a complication in the neck of the shoulder-organ. Its opening is oblique, like that of a hypodermic needle, and its duct is supported by a tubular reinforcement, a modified scale or thin bone (? rudimentary post-cleithrum). This skeletal structure is flexible, and penetrates deeply towards the sac of the shoulder organ. Its presence in small Searsids in which the squamation is undeveloped rather points to its being a specialized bone. I have not proceeded further with this investigation for the present, since most of the British Museum material is taxonomically significant as well as scanty, and haphazard dissection undesirable.

Parr (1937) first attached systematic importance to the shoulder organ in erecting the genus *Searsia*. In his latest publication (1951) he omits mention of reinforcement of the external tube, but adds certain information to Beebe's earlier account :

> " The sac is lined with black integument and traversed from outer to inner wall by irregular strands or columns of soft tissues. There can be no doubt that this represents a secretory organ, and it seems quite likely that its function may be to secrete a luminous mucus. The sac discharges through a tube, also lined with black tissue . . . (this tube) is apparently quite strong since it seems to withstand considerable abrasion and the loss of all scales."

Is it not possible to go further than this, on the anatomical evidence now available ? Everything points to the shoulder organ being a structure for the reception of luminous particles *which are effectively blacked-out by the densest pigment in the body until required, and then expelled in a jet to form a luminous protective cloud*, as in the squid *Heteroteuthis dispar* and in several deep-sea crustacea—*Acanthephyra pellucida*, *Heterocarpus alfonsi*, *Pandalus alcocki*, *Aristaeus coruscans*, etc. (For encyclopaedic bibliography see Newton Harvey, 1952, *Bioluminescence*. New York). It is true that a *ductus ejaculatorius* or muscles in the wall of the sac have yet to be demonstrated, but even in the absence of these a mesiad movement of the cleithrum could readily induce ejaculation : very light pressure on the pectoral girdle of a preserved specimen produces a strong current of preservative fluid.

If this case is established it is the first instance of a luminous cloud-thrower to be found among fishes. Ventral saccular luminous organs are known in many Macrourids and in *Physiculus* among the Gadids (references in Newton Harvey, *ante*), but anatomical evidence and field observation in these cases point to incomplete concealment of the luminous contents of the glands, and to a gradual emission of luminous slime onto the body.

(2) *Light organs*

Light organs in animals are known or believed to subserve a variety of functions : attraction of prey ; diversion and confusion of pursuing predators ; local environment illumination as an aid to vision ; neuro-facilitation of the optic nerve ; self-indication of the state of the whole photophore system by means of " pilot lights " ; intra-group (species) recognition ; sex recognition, advertisement and maturity indication. So much is generally known, but it does not seem to be as generally realized that the relative evolutionary potentialities and consequent taxonomic significance of each type of photophore system must vary very widely in relation to the function performed.

In many cases selection-pressure will favour lighting systems having greater efficiency, and consequently bring about the convergent evolution of similar arrangements in unrelated groups. Analogous luminous cloud-projection devices in squids, crustacea and fishes have been discussed in the previous section (p. 199) ; special modification of homologous structures may also be replicated, as for example the terminal photophores on the first dorsal rays of *Chauliodus* and the Ceratioid Angler-fishes and the minute light organs on the eyeballs of *Chauliodus*, *Persparsia* and certain new Myctophids in the " Rosaura " Collection.

Once a luminous organ or organ-complex has attained a certain measure of efficiency, selection-pressure may, while maintaining that standard, permit such variation in detail as does not detract from the usefulness of the whole. Thus it happens that in the illicium (esca) of the Ceratioids and in the mental barbel of the higher Stomiatoids there is considerable inter-specific (and, to an unknown extent, intra-specific) variation. In the latter group it has sometimes been possible, without affecting the attractiveness of the mental barbel to prey, to superimpose a sexual dimorphism and thus fulfil two functions with the same structure.

Only in the case of recognition marks is there a strong tendency towards differentiation of photophore patterns, and that in definite steps with a rigorous disciplining of the range of variation at each stage. Selection-pressure in favour of such differentiation is least intense under conditions of allopatric speciation (which in the marine habitat has great possibilities in the third dimension, e.g., bathymetric stratification of species of *Cyclothone*) and strongest under conditions of sympatric speciation. The tendency is well demonstrated by the wide divergences between the fundamental photophore patterns of the deep-sea squids, the several families of Stomiatoid fishes and the Myctophids, and by the wonderful diversity within each of these groups.

It follows, therefore, that in cases where there is reason to believe that intra-species recognition is the primary function of a photophore system the variations of that system may be expected to provide the most sensitive index of speciation. Moreover, variations in recognition patterns, like variations in physiological tolerances, breeding behaviour, etc., themselves constitute isolating factors, and may thus precede or even initiate further genetic and therefore morphological differentiation of populations.

Conversely, if, after making due allowance for the disparity between the taxonomist's and the animals' assessment of a variation, that variation does not seem likely to be clearly characteristic at a distance, then one should be reluctant to apply it as an index of speciation in sympatric populations.

Having stated these general principles we may now consider the light organs in the two species introduced by Parr (1937) as *Searsia koefoedi* and *S. polycoeca*. Modest and probably relatively inconspicuous as photophore systems go, clearly distinguishable from the basic patterns of the Myctophidae and Stomiatoidea by their very economy, localized at a few points along the ventral surface, there can be little doubt that their primary function is intra-specific recognition. Yet in these two species the fundamental patterns are, in lateral view, absolutely identical (assuming no difference of colour) : five lights placed at equivalent points along a straight line. Only in ventral view does the relatively subtle difference in disposition and relative sizes of the subventrals and postventrals appear (cf. Parr's figs. 4 and 5), and although the eyes of Searsidae have probably a wide field of vision (particularly in the young stages ; my Text-fig. 19), there is no such obvious connection between upward binocular vision and downwardly directed photophores, as can be demonstrated in the Sternoptychidae. The differences between the lateral views of the photophore systems in these two species and in *Persparsia*, another genus of the same family (*post*, p. 209) support the case for lateral distant recognition.

Beebe, (1926, *The Arcturus Adventure*, N.Y. : 216, pl. 5) has very beautifully illustrated the sexual dimorphism in *Myctophum coccoi* ; the male has conspicuous luminous scales along the upper side of the tail and the female along the lower side. To me the divergence between *Searsia koefoedi* and *S. polycoeca* for long seemed of much the same order and likely significance ; a divergence of far less use than that in *Myctophum* as a means of recognition at a distance, but of likely utility in identifying the sexes to one another in a group of individuals of one species brought together by the general species recognition pattern of the remaining photophores. On that hypothesis I made a considerable effort (Table II) to justify the treatment of *S. polycoeca* as a synonym of *S. koefoedi*, but after the examination of material of each I am driven to accept them as distinct species. It will be interesting to see whether the promised ' Dana ' Report on the Searsidae will fulfil the prediction now made that the Atlantic populations of these two species will prove to be geographically and/or bathymetrically isolated.

Although this hypothesis of sexual dimorphism in *Searsia* has proved unfounded, the general similarity of the photophore patterns remains a powerful argument against the removal of *S. polycoeca* to another genus—*Holtbyrnia*—and within that genus to a sub-genus *Mentodus* containing one other species, *H.* (*M.*) *rostratus* (Günther), said to be known only from a unique holotype devoid of photophores.

The last-mentioned specimen has been badly cut about by successive investigators, but there is no doubt that it originally possessed no trace of light organs. The ventral squamation is complete and intact except at those points where exploratory borings have been made, and experiments on specimens of the more plentiful *Persparsia taaningi* indicate that abrasion of the photophores without damage to the body is highly unlikely. All the specimens identified as "*Bathytroctes rostratus* Günther" by other authors and examined by Parr have proved to be either *S. koefoedi* or *P. taaningi.*

Parr (1937) supports his argument against ontogenetic atrophy of the light organs in *B. rostratus* by citing from the literature a series of Searsids of ascending size in which those structures are present, including one (unfortunately not figured by its original author) of equivalent size to Günther's holotype. The critical specimen is still 10 mm. S.L. shorter than Günther's, and this may, in terms of age, be rather more significant in fishes apparently near their limit and presumably growing at a correspondingly slower rate. However, Krefft (1953, see my footnote, p. 206) in a paper received while the present was in the press, describes a photophore system constant in number and arrangement through a series from 87–174 mm. S.L. .

A specimen in our collections from "Discovery" St. 2074 (21.ix.37. 10° 10′ N., 21° 13′ W.; closing net, oblique haul; 875–400 metres, sounding 5,148 metres) bears a label "*Holtbyrnia polycoeca* Id. A. E. Parr." The salient characters of this fish are given in Table II, where it will be noted that it gives good agreement with the holotype of that species in all characters except the head length, which runs contrary to the expected allometry. There are, however, discrepancies in the light organs. The supraventrals and supra-anals are present and typical, but the posterior anals are marked only by small patches of dark pigment, the median subcaudal is very faint and has only a trace of pigment, the thoracic organ is very thin if it is present at all, and the subventrals and postventrals are altogether wanting. Since the specimen is in excellent condition I am inclined to regard the photophore system as undergoing degeneration.

(3) *Notes on taxonomy of Searsids*

Beebe (1933) has interpreted Günther's (1887) figure of the snout of *Bathytroctes rostratus* in terms of the typical Searsid condition with forwardly directed tusks, and this interpretation was at first disputed by Parr (1937). On examining the specimen I find the premaxillaries thin and somewhat eroded, but the terminal lip-like projections are still present and prove to be hollow and capable of admitting a bristle for a fair distance. I regard these structures therefore as representing the broken stumps of tusks with their related pulp-cavities; alternatively and less probably, as the premaxillary sockets of tusks which have been shed (see also p. 208). The increased number of accessory teeth is a function of age and size, while the elaborate crenellation of the edge of the jaw is of a type common on the edges of thin bones which have completed their major growth, comparable, for example, with the elaboration of the skull crests in *Melamphäes*.

Parr has also complained that Beebe (1933) shows a shoulder organ in a figure stated to be based on Günther's when the original and description do not include it. Perhaps Beebe saw the specimen at some time and erred only in the legend to his figure, otherwise it must appear very odd that both Beebe and Parr are correct; there is a shoulder organ present in the specimen, though not shown in the original figure. Only the tip of the tube, with its internal support, projects from the body, but the sac must still be quite large, for a fair amount of preservative fluid and air bubbles can be extruded from the tube by exerting moderate pressure on the shoulder girdle.

Parr (1951) modifies his earlier standpoint on this species by placing *B. rostratus* fairly among the Searsidae as *Holtbyrnia* (*Mentodus*) *rostratus*. Though he does not elaborate his reasons in what, after all, only purports to be a preliminary revision, we can fairly assume that he has made the above observations during one of his vists to the British Museum (Natural History).

The principal characters of three species of Searsids are tabulated in Table II. A number of identical or nearly identical features are omitted for brevity's sake, but all the salient points have been included.

Principal specific differences relate to the light organs (already discussed p. 201), the proportions of the head and upper jaw to standard length, the gill-raker counts, presence or absence of a dermal pit behind the shoulder, and the number and nature of the pyloric caeca. Having tested and rejected the hypothesis that *S. koefoedi* and *S. polycoeca* were sexes of the same species, I hoped at least to find support for a theory that *S. polycoeca* was a young stage of *B. rostratus*. Unfortunately this idea must be rejected also, although I am satisfied that *B. rostratus* and *S. polycoeca* are very closely related, and confidently expect that the young stages of *B. rostratus* when found will prove to possess photophores. I would advocate the inclusion of all three of these species in the genus *Searsia* as the expression of this close relationship.

The importance to be attached to the pyloric caeca may be questioned. Considering Parr's figures of the pyloric caeca in *S. koefoedi* and *S. polycoeca* (1937, figs. 1A & B), it may be seen that there is a fundamental similarity between them, for both have five primary caeca along the right side of the stomach and a further group of three along the anterior end adjoining these. Even the condition in *S. rostratus* which has been described as having " 14 simple, straight pyloric appendages " can be reduced to this same basic pattern. Although the immediate impression is of fourteen simple caeca (11 + 3) packed side by side like the fingers of some polydactyl hand, closer inspection shows that there is one group of five primary caeca, of which the anterior one forks twice, the second, third and fourth once each and the last is simple, like the remaining group of three. The forking takes place very close to the stomach, and the sum of the terminal diverticula, 1.1.1.4.2.2.2.1, gives the total of 14. It may fairly be asked how much variation is due to individual differences and to ontogenetic changes? The new specimen of *S. polycoeca* presents a much simpler picture than the smaller holotype, while the

TABLE II.—*Data for Types of* S. koefoedi *and* S. polycoeca *compiled from Parr* (1937, 1951) ; *remainder original*

	Searsia rostratus	*Searsia koefoedi*				*Searsia polycoeca*	
	(Holotype) " Challenger " St. 120. 8° 33′ S., 34° 30′ W.	(Holotype) " Pawnee " St. 18. 23° 39′ N., 76° 41′ W.	(Paratype) " Pawnee " St. 9. 23° 55′ N., 77° 09′ W.	" Discovery " St. —. 13° 25′ N., 18° 22′ W.	" Rosaura " St. 46. 7° 27′ N., 23° 08′ W.	(Holotype) " Pawnee " St. 58. 32° 24′ N., 64° 29′ W.	(?) " Discovery " St. 2074. 10° 10′ N., 21° 13′ W.
Standard length mm.	148	69	47	46·5	15·5	48	72
Percentages of S.L. :							
Head	33·1	30·4	29·8	31·3	34·1	27·0	36·1
Eye	8·7	10·0	10·6	9·6	11·6	10·4	10·4
Maxillary	19·2	14·5	14·9	16·1	16·7	20·8	20·5
Lower jaw	20·9	*ca.* 19·2	. .	18·9	21·9	21·5	22·9
Snout	8·7	8·0	7·0	7·5	8·3	9·4	9·7
Depth	21·0	19·0	17·0	16·7	18·0	19·0	25·0
Snout—dorsal	62·8	64·5	64·0	60·2	66·4	64·5	65·2
Snout—ventral	54·7	51·0	51·0	48·6	60·0	55·0	56·2
Dorsal base	19·0	18·5	20·1	20·0	16·1	17·7	20·0
Anal base	16·5	17·0	18·5	17·2	12·9	15·6	17·0
Gill-raker	5·4	4·4	. .	4·8	1·3	4·7	6·8
Radial formula	D.20 ; A.18 ; P.18/17 ; V.9	D.21 ; A.20 ; P.23 ; V. ?	As holotype ?	D.21 ; A.20 ; P.20 ; V.7	D.20 + ; A.17 + ; P.20 ; V.7	D.20 ; A.17 ; P.22–3 ; V. ?	D 21 ; A.17 ; P.20 ; V.8
Branchiostegal rays	8	. .	. .	7	7	. .	8
Vertebrae (radiograph)	49	. .	. .	. .	. .	. .	. .
Gill-rakers on first arch	8/1/20 (L.) 10/1/21 (R).	7/1/19 (1937) 29–35 (1951)	As holotype ?	8/1/18	0/1/9	6/1/15	6/1/15
Lateral line scales	*ca.* 110–120 (caudal tip torn)	About 85 (1937) 80 to 100 (1951)	,,	*ca.* 80	Absent	Absent	*ca.* 90
Shoulder organ	Present	Present	Present	Present	Present	Present	Present
Dermal pit behind shoulder girdle	Absent	Absent	As holotype ?	Absent	Absent	No mention (1937) Present (1951)	,,
Lateral line pores before post-temporal	Few present	,,	,,	,,	,,	Numerous	Numerous
Urinogenital papilla	Present	Present	,,	Present		Absent ?	Present

Photophores	No trace	1 linear thoracic, 2 supraventrals, 2 subventrals, 2 postventrals, 2 supra-anals, 2 postero-anals, 2 subcaudals. (Details in Parr, 1937.) 1 ocular fig., ? not desc. (1937)	,, ,,	As in the holotype, but the subventrals seem to have coalesced. ? sex-difference 1 antero-dorsal ocular ?	None developed	1 linear thoracic, 2 supraventrals, 2 subventrals (vague), 2 postventrals (large), 2 supra-anals, 2 postero-anals, 2 subcaudals. (Details in Parr, 1937.) No ocular ?	? Thoracic 2 supra-ventrals subventrals atrophied postventrals atrophied 2 supra-anals 2 postero-anals (faint) 2 subcaudals (faint) No ocular ?
Maxillary reaches to posterior margin of orbit ?	Yes	No	,,	No	No	Yes	Yes
Dentition :							
Premaxillary tusks (1–1)	Broken or shed	Present	,,	Present (2 on left side)	Not erupted	Present	Present
Vertical teeth below each tusk	,, ,,	2	,,	2	1	1	1
Other premaxillary teeth	14–15	4–6	,,	4–5	5	4	4
Maxillary teeth	About 50	40–50	,,	About 30–40	10+	20–25	Mx. eroded
Dentary teeth :							
Main series	About 50–60	Numerous	,,	Numerous	Numerous	?	Numerous
Outer series	6–9, strong	Short series or none	,,	Rudiments	2 + rudiments	Few, minute	Few rudiments
Vomerine teeth	2	2	,,	1	2	2	2
Palatine teeth	0–1	0	,,	0	1	2	1
Pyloric caeca	" 14 simple, straight pyloric appendages " (Parr, 1951) 8 primary caeca, with 12 secondary branches and 14 terminal diverticula—(D.W.T.)	8 primary caeca, with 15 secondary branches and 19 terminal diverticula. (Data from fig., 1937)	,,	5 primary caeca, with 12 secondary branches and 13 terminal diverticula	Damaged in dissection. Many small diverticula	8 primary caeca, with 16 secondary branches and 25 terminal diverticula. (Data from fig., 1937) " 6–8, some branched, but fewer than 10 terminal diverticles." (Parr, 1951)	6 primary caeca, with 12 secondary branches and 13 terminal diverticula

larger new *S. koefoedi* is markedly different from the holotype of that species. It may well be that the primary forks remain as they are, while the total of tertiary divercula becomes reduced by subsequent growth at the secondary forks.

The British Museum (Natural History) now possesses the following material of this family :

1 *Searsia rostratus* (Günther) Holotype.
2 *Searsia koefoedi* Parr.
1 *Searsia polycoeca* Parr.
5 *Persparsia taaningi* Parr.
1 *Normichthys operosa* Parr.
1 *Pellisolus facilis* Parr.

As regards Parr's draft classification of 1951, I would modify it as already indicated to show the supposed affinities of the three species which I place in *Searsia.* There arises another problem, common enough when reticulate evolution has to be expressed in a two-dimensional classification, of indicating the affinity which appears to exist between *Normichthys operosa* and *S. polycoeca* alone among the *Searsia* group. *Normichthys* has a row of six large pits behind the shoulder, each containing three opaque white bodies (? photophores or sense-organs ?), as well as a smaller pore in every scale of the body. The single dermal pit behind the shoulder of *S. polycoeca* seems to be the precursor of such a condition.

The grouping adopted in the key according to relative size of head and length of upper jaw is useful enough for taxonomic purposes, but does not impress me as a natural phyletic classification, for the reasons which have already been indicated.

Searsia koefoedi Parr[1]

(Text-fig. 17)

Parr, 1937, *Bull. Bingham Oceanogr. Coll.* **3** : 16, Fig. 4 ; Maul, 1948, *Bol. Mus. Municipal Funchal,* No. 3, Art. 5 : 12, Fig. 3 ; Parr, 1951, *American Mus. Novitates,* No. 1531 : 17.

Bathytroctes (*Talismania*) *homopterus* (non Vaillant) (part) Norman, 1930, "*Discovery*" *Reps.* **2** : 269 (not fig.).

St. 46. 30.xii.37. 7° 27′ N., 23° 08′ W. 2-metre Stramin Net, 1000(–0) metres. 1 specimen, 15·5 mm. S.L. Reg. No. 1953.3.6.12.

Hab. North and South Atlantic ; Caribbean.

A young fish and contorted, its body bent downwards from behind the nape and its tail curved forwards along the left flank. The following information expands and supplements that given in Table II.

D.20 + ; A.17 + ; P.20± ; V.7 ; C.7 + : XXII : 5 +

Branchiostegal rays 7. Gill-rakers on first arch 0/1/9.

Proportions in per cent of length without caudal (S.L.) : length of head, 34·1 ; snout, 8·3 ; orbit, 11·6 ; interocular width, 7·0 ; upper jaw, 16·7 ; premaxillary, 4·5 ; posterior supramaxillary, 5·8 ; lower jaw, 21·9 ; snout to ventrals, 60·0 ; snout to dorsal, 66·4 ; snout to anal, 70·9 ; greatest depth of body, 18·0 ; least depth of caudal peduncle, 6·4 ; dorsal fin base, 16·1 ; anal fin base, 12·9.

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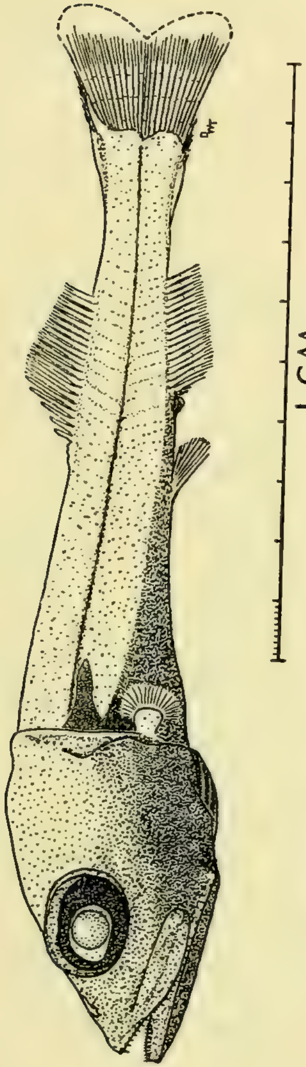
[1] A paper by Krefft (1953, *Zool. Anz.* **151** : 259–266) received while the present work was in the press, describes as new *Searsia schnakenbecki* from Iceland.



TEXT-FIG. 17. Young *Searsia koefoedi*, 15·5 mm. S.L. from "Rosaura" St. 46.

Least depth of caudal peduncle 35·7 per cent of greatest depth of trunk.

0·0625 S.L. = 0·97 ; 0·0375 S.L. = 0·58 (data for Parr's formulae).

DENTITION. Only the extreme tip of the forwardly directed tusk on the premaxillary is yet erupted. One downwardly directed fang at the front of each premaxillary, followed by five slightly smaller teeth which are fairly regularly spaced. Ten similar teeth on the maxillary, with indications of smaller teeth to be erupted between and within these. One pair of fangs on vomer, the largest teeth yet developed. One slender tooth on each palatine. On the dentary a single row of numerous very fine teeth, with a few (4–5) larger vertically directed ones outside these and probably of the same series. Of the horizontally directed series two teeth are erupted at the front end of each dentary and others unerupted may be seen opaque white in the jaw. A tiny projection below the dentary symphysis.

EYES. The orbits are slightly longer than high. The eyes project some way beyond the general contour of the head and must have wide and partly coincident fields of vision. The lens is pale green, large but slightly smaller than the pupil as fixed. There is a greyish-white retinal tapetum lucidum, which may be luminous.

COLOUR. Dorsally light brown, ventrally dusky. Outer integument over shoulder organ granular dark brown, with darker internal pigment of tube showing through. A darker triangular patch between the shoulder organ and the pectoral fin. A dark line along the lateral line. Fin bases pale.

There are no certain indications of light organs. The fins are well advanced, but the full complement of anterior dorsal rays, procurrent caudal rays, and possibly of anterior anal rays, is not complete. Gill-rakers moderately long and widely spaced ; their complement also incomplete. Lateral line pores before ascending limb of post-temporal.

This specimen agrees very well with *Searsia koefoedi* in all general proportions. The relative distances from snout to dorsal and anal differ by 4·3% (" less than 4% ")—a trivial difference against the likely error in measuring a difficult specimen. Lower counts for teeth, fin-rays and gill-rakers reflect the relatively small size of the fish, and in some respects show an approach to *S. polycoeca*.

Of the three specimens referred to *Bathytroctes* (*Talismania*) *homopterus* Vaillant by Norman (1930), the largest, from " Discovery " St. 269, proves to be *Normichthys operosa* Parr, as already noted in Parr (1951). The second specimen, from the same station, seems no longer to be in this Museum. The third, from an unnumbered " Discovery " station, is a fine *Searsia koefoedi* whose characters are given in Table II. It is of interest to note that in this specimen the left premaxillary tusk is laterally duplicated, which may be an indication of periodic replacement and so provides a possible explanation of the tusk-less condition of the holotype of *Searsia rostratus*.

Persparsia taaningi Parr

(Text-figs. 18 and 19)

Parr, 1951, *American Museum Novitates* No. 1531 : 18.

Bathytroctes rostratus (*nec* Günther) Norman, 1930, " *Discovery* " *Reps.* **2** : 268, Fig. 1 ; Pl. 2, Fig. 3 ; Beebe, 1933, *Zoologica, N.Y.* **16** : 43, Figs. 8C, 8D.

Searsia n. sp. Parr, 1937, *Bull. Bingham Oceanogr. Coll.* **3** : 16.

St. 33. 22.xi.37. 11° 00′ N., 75° 43′ W.; 2-metre stramin net; *c.* 1,200(–0) metres. 1 specimen, 23 mm. S.L. Reg. No. 1953.3.6.13.

HAB. North and South Atlantic; Caribbean.

A young fish and badly contorted, the posterior half of the body twisted and bent forward to lie along the left cheek.

D.21; A.14; P.20 ±; V.8; C.3 + : XXII : 2 +.

Branchiostegal rays 7. Gill-rakers on first arch 4/1/12.

Proportions in per cent of length without caudal (S.L.): length of head, 40·0; snout, 10·8; orbit, 13·9; interocular width, 6·0; upper jaw, 20·8; premaxillary, 6·5; posterior supramaxillary, 7·8; lower jaw, 25·2; snout to ventrals, 62·1; snout to dorsal 63·4; snout to anal, 71·3; greatest depth of body, 16·5; least depth of caudal peduncle, 6·5; dorsal fin base, 20·4; anal fin base, 12·1.

Least depth of caudal peduncle 39·4 per cent of greatest depth of trunk.

0·0625 S.L. = 1·437; 0·0375 S.L. = 0·862 (data for Parr's formulae).

DENTITION. The forwardly directed tusks are present but not erupted. The premaxillaries are very thin and their edges damaged; teeth that remain at the hinder ends are like those of the maxillary. The maxillary has about 20 teeth with indications of very fine ones between these. Four fangs on vomer, the largest teeth yet developed. Two slender teeth on each palatine. The dentary has a small upwardly directed projection at the symphysis and many acicular teeth in a single row.

EYES. The eyes and orbits are elongated. The eyes project some way beyond the general contour of the head, and must have wide and partly coincident fields of vision, especially in the upward direction (Text-fig. 19). The lens is pale green and as large as the pupil as fixed. There is a greyish-white retinal tapetum lucidum.

COLOUR. Dorsally light brown, ventrally dusky. Integument over shoulder organ dark brown. A dark line of pigment along the lateral line. Fin bases pale.

There are no certain indications of light organs. Gill-rakers long, the longest 0·9 mm. (3·9% S.L.). Gill-filaments numerous, short and stumpy. No lateral line pores before ascending limb of post-temporal.

This fish shows a number of small divergences from Parr's diagnosis (1951), especially in the slightly longer head, longer lower jaw, and more posterior insertion of the ventrals. In view of the youth and twisted condition of the specimen it seems better not to attach much importance to these differences in face of the general agreement with *P. taaningi*.

Norman's (1930) figures from "Discovery" specimens which I identify with this species do not do full justice to the photophore system. In addition to those shown in his drawings and plate there are: two light organs on the eyeball,[1] in the upper and lower anterior corners; one on the skin over the lower posterior edge of the orbit; one near the hinder edge of the operculum, above the level of the pectoral fin base; in the largest specimen (47 mm. S.L.) a median one at the lower ends of the cleithra, and in the same specimen an additional median photophore between the supraventrals (not to be confused with the curious two-way light

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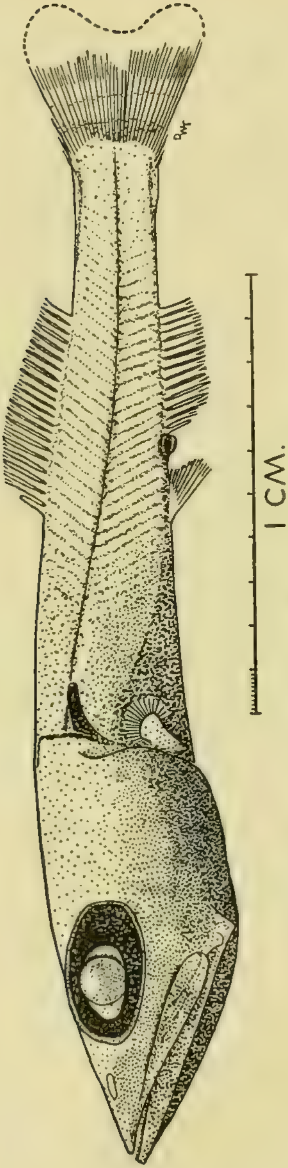
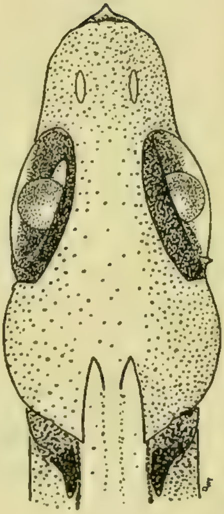
[1] *Searsia schnakenbecki* Krefft (1953) has a photophore on the eyeball. Parr (1937) seems to figure one in *S. koefoedi* though he makes no mention of it in his text.



TEXT-FIG. 18. Young *Persparsia taaningi*, 23 mm. S.L. from " Rosaura " St. 33.



TEXT-FIG. 19. Dorsal view of head of young *Persparsia taaningi* shown in Fig. 18.

organ already noted by Norman). In addition to these special organs there are likely indications of a strip of luminous tissue extending from the occiput to the dorsal, and elsewhere about the fin bases. The few specimens available are small, and, while they provide indications that the light organs are not developed simultaneously, they are inadequate for a study of possible sexual dimorphism. The light organs on the eyeball are quite inconspicuous in the largest specimen available, but there is otherwise no evidence to support ontogenetic atrophy; on the contrary. Doubtless Parr will be dealing with this matter in full in his forthcoming monograph.

Family CLUPEIDAE

Pellonula afzeliusi Johnels

Johnels, 1954, *Arkiv. f. zool. Stockholm* (2) **6** : 352.
Pellonula vorax (*non* Günther) Svensson, 1933, *K. Svensk. Vetensk. Handl.* (3) **12**, No. 3 ; 47, fig. 16 (young stages).

St. 48. 3.i.38. 13° 27′ N., 15° 47′ W.; 2-metre stramin net, 3(–0) metres. 526 specimens, 4–81 mm. S.L. Reg. No's. 1953.3.6.14–541.

HAB. Gambia River.

Apart from the other characters noted by Johnels, this species differs from *P. vorax* in the possession of much more trenchant keeled scutes between the isthmus and the ventrals.

Harengula pensacolae Goode & Bean

Clupea humeralis (part) Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 422 ;
Harengula pensacolae Goode & Bean, 1879, *Proc. U.S. Nat. Mus.* **2** : 152 ; Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 389.

St. (—) 28.x.37. 17° 28′ N., 88° 11′ W.; dip-net, at surface. 5 specimens, 60–98 mm. S.L. Reg. No's. 1953.3.6.542–6.

HAB. Gulf of Mexico ; Caribbean.

Ilisha africana (Bloch)

Clupea africana Bloch, 1795, *Naturgesch. Ausländ. Fische*, **9** : 45, pl. 407. (Type loc. Accra, Gold Coast.)
Clupanodon africanus Lacépède, 1803, *Hist. Nat. Poissons*, **5** : 469, 471.
Pellona iserti Cuvier & Valenciennes, 1847, *Hist. Nat. Poissons*, **20** : 307.
Pellona gabonica Duméril, 1858, *Arch. Mus. Paris*, **10** : 259, pl. 23, figs. 3, 3a.
Pellona africana Bleeker, 1863, *Natur. Verh. Holl. Maatsch. Wetensch.* (2) **18** : 122, pl. 27, fig. 1.
Pristigaster dolloi Boulenger, 1902, *Proc. zool. Soc. Lond.* : 271, pl. 30, fig. 3.
Ilisha melanota Derscheid, 1924, *Rev. Zool. Afr.* **12** : 278 ; Irvine, 1947, *The Fishes & Fisheries of the Gold Coast*, London : 111, fig. 39.
Ilisha dolloi Giltay, 1935, *Bull. Mus. roy. Hist. nat. Belg.* **11**, fasc. 36 : 3, figs. 1 and 2.
Ilisha africana Fowler, 1936, *Bull. Amer. Mus. nat. Hist.* **70** : 178, fig. 71. Delsman, 1941, *Mem. Mus. roy. Hist. nat. Belg.* (2) Fasc. 21 : 50.
Pristigaster martii (*non* Agassiz) Fowler, 1936, op. cit. : 180, fig. 72.
[*non Pellona africana* Günther, 1868, Cat. Fish. Brit. Mus., **7** : 455.]
[*non Ilisha africana* Norman, 1922, Ann. Mag. nat. Hist. (9) **11** : 4.]

St. 48. 3.i.38. 13° 27′ N., 15° 47′ W. 2-metre stramin net, 3(–0) metres. 2 specimens, 84–102 mm. S.L. Reg. No's. 1953.3.6.547–8.

HAB. Coastal waters and estuaries of W. Africa, Senegal to Angola.

Norman (1922) includes *Ilisha africana* in the first section of his key to the genus *Ilisha*:

> " I. Less than 46 scales in a longitudinal series; 16–20 scutes before insertion of pelvics."

Bloch (1795) does not supply this information, but counts from his figure give 46 and 24 + respectively, and therefore rather better agreement with the second section of Norman's key:

> " II. More than 46 scales in a longitudinal series; 20–28 scutes before insertion of pelvics."

At the time when Norman wrote, the British Museum (Natural History) did not, in fact, possess any material of Bloch's species, nor indeed any belonging to the genus *Ilisha* and of undoubted African origin. Norman followed Günther (1868) in mistakenly identifying with Bloch's fish a single specimen, B.M. (N.H.) No. 1852.9.13.175, which came originally, and without any locality data whatsoever, from the collections of the Zoological Society. This specimen should be assigned to *I. indica* (Swainson) or *I. brachysoma* (Bleeker), two doubtfully distinct species from India and the East Indies, from which region it very probably came. Its ventral scutes (20 + 8) give a lower pre-pelvic count than in any African *Ilisha* known, and are much less salient than those in the copious African material of *I. africana* (Bloch), (including specimens from Accra, the type locality), received at this Museum in recent years.

Norman's error has effectively bedevilled every subsequent author except Fowler (1936), who providentially overlooked his paper in the main body of *The Fishes of West Africa* and later mentions it without comment in an "*Appendix*" to this work.

Derscheid (1924) leaned heavily upon Norman's revision and advice and (Bloch's book being extremely rare) seems not to have checked the original description and figure of *I. africana.* Taking very literally Norman's statement that *I. africana* (non Bloch) is " scarcely distinct from *I. brachysoma*," Derscheid has apparently deduced a pseudo-description of the genuine *I. africana* by so modifying Norman's detailed account of *I. brachysoma* as to reconcile it with the few minor differences noted by Norman in his brief comments on a supposed *I. africana* which was, as we have seen, not Bloch's species. Derscheid then proceeds to detail the differences between his African material from the mouth of the Congo and this pseudo-*I. africana* whose antecedents, if they may be said to have any reality at all, are Asiatic. Naturally enough he fails to recognize his own material as the genuine *I. africana* (Bloch) and so *I. melanota* joins the lengthening list of synonyms. *Ex Africa semper aliquid novum*!

Giltay (1935), having examined the types of *I. melanota* Derscheid and of *Pristigaster dolloi* Boulenger (1902), makes *I. melanota* a synonym of *I. dolloi* (Boulenger).

This view will be supported in greater detail presently; for the moment it is merely emphasized that Giltay did not carry his synonymy back any further than Boulenger (1902), and merely includes "*Ilisha africana* Norman . . . (pro parte)" as an allusion to Norman's tentative synonymy of *P. dolloi* Boulenger with *I. africana* (Bloch).

Fowler (1936) overlooked Derscheid's paper as well as Norman's, and consequently makes no contribution to the *brachysoma-africana-melanota* tangle. Indirectly, however, he adds to the confusion by making *P. dolloi* Boulenger a synonym of *Pristigaster martii* Agassiz (Spix & Agassiz, 1829, *Pisc. Brazil*: 55, pl. 24*a*) and presenting a re-drawn version of Boulenger's figure of 1902 as "*Pristigaster martii*, modified from Boulenger." Ludicrous as it may seem after a comparison with the original figures, the error is liable to prove as dangerous as Norman's, for Spix & Agassiz is almost as rare a work as Bloch.

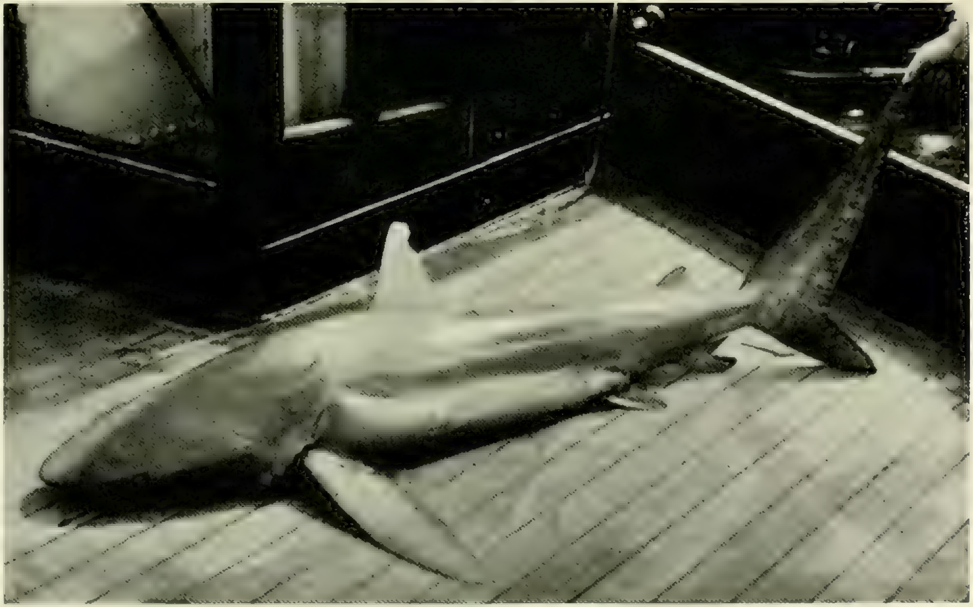
Delsman (1941) has questioned the validity of *I. melanota*, but upon the same false premises as led Derscheid to erect his species. Delsman concentrates upon the ventral scutes, which Derscheid gives as 18–20 + 7–8 in his pseudo-*I. africana* based on Norman's account of *I. brachysoma* and 25–27 + 7–8 in *I. melanota*, and endeavours to close the imaginary gap by citing counts of 22–24 + 7 from new material. Bloch's original figure (1795) shows *ca.* 24 + 5; if there is any problem it is presented by the post-pelvic rather than the pre-pelvic count, and if we allow the artist a small error in the pelvic fin insertion we can reconcile this difference without compromising the opening argument in the present article, for it is possible to postulate a correction from *ca.* 24 + 5 to *ca.* 22 + 7 without even invoking the probable scutes concealed by the operculum in Bloch's figure.

Norman (1924), Giltay (1935) and Delsman (1941) have all, from their several concepts of *I. africana*, queried the distinctness of *Pristigaster dolloi* Boulenger (1902). Boulenger introduced this species with a brief description and figure, and no discussion. Derscheid (1924), having compared the type of *P. dolloi* with his types of *I. melanota*, is unable to discover any other important difference than that the former lacks even the rudiments of pelvic fins. Giltay, working also from original material, gives an intensive comparison, together with a theoretical dissertation on the body-forms of fishes which, curiously enough, fails to make the obvious comparison with the Gastropelecidae. Giltay's very valuable contribution is to cite the work of Pellegrin (1926, *C.R. Acad. Sc. Paris*, **183**: 1301) who examined 13 specimens of the African Clariid *Clariallabes variabilis* Plgr. and found 6 with both ventrals present, 2 with one only, and 5 with none. Hildebrand (1943, *Bull. Bingham Oceanogr. Coll.* **3** Art. 2: 140) reports 1 specimen lacking ventrals among 20 *Pterengraulis atherinoides* (L.) examined by him. Considering such precedents, the minute pelvic fins in *Ilisha*, and the close correspondence between Boulenger's unique holotype of *P. dolloi* and the many African specimens of *Ilisha* now examined by several authors, there exist no reasonable grounds for retaining Boulenger's species as distinct.

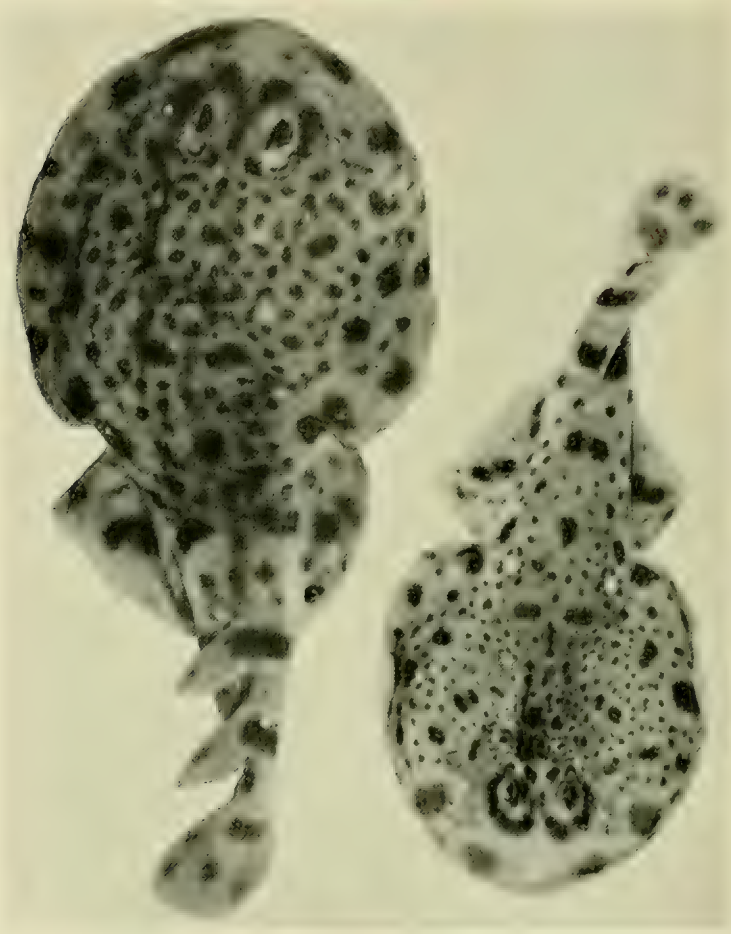
The considerable African material of *I. africana* (Bloch) received at the British Museum since Norman's time may properly be referred to *Ilisha* Gray & Richardson as generally understood, since it possesses a maxillary not adherent to the premaxillary, and rounded at the posterior end ; a ligament rather than a bone between the maxillary and premaxillary (but see Myers, *Copeia*, **1950** : 63), and no canine teeth.

A new world-revision of *Ilisha*, desirable as it appears, cannot be undertaken in the middle of a general report. I state therefore only a general impression that, on the material which I have handled for comparative purposes, there may be a case for recognizing the distinctness of *Ilisha africana* from the Indo-Pacific forms by the creation of a new sub-genus. Compared with *I. brachysoma*, *I. indica*, *I. kampeni*, *I. sladeni*, etc., it shows the following differences : the ventral scutes are far more salient ; the lower jaw projects further, so that the mouth opening is carried further dorsad ; the lower part of the body (ventral to the lower jaw) is more developed and keel-like, so that the overall body depth is greater and the pectoral fin, though maintaining the same relations to the head, is inserted proportionally higher ; the pectoral fin, though obliquely inserted, tends to twist so as to project in a horizontal plane perpendicular to the surface of the body. In these same characters it approaches the related genera and species of the Atlantic coasts and rivers of South America.

Perhaps the most interesting feature of *Ilisha africana* is that in the development of the deep ventral keel, in the carriage of the pectoral fins, elongation of the anal, exaggeration of the lower lobe of the caudal, and incipient loss of the pelvics, (though not in the normal lateral septum), it foreshadows the form and probably also the habit of the Gastropelecidae—South American Ostariophysi which " fly " by " a taxi-ing movement, with the large thoracic keel cleaving the water and the pectoral fins beating the surface " (Fraser-Brunner, 1950, *Ann. Mag. nat. Hist.* (12) **3** : 959). These characteristics of *I. africana* attain a full convergent evolution of the Gasteropelecid condition in the related South American *Pristigaster cayanus* Cuvier (1817, *Règne Animal*, **4**, pl. 10, fig. 3). (*P. martii* Agassiz is a synonym of this species.) Parallel evolution of the same condition has occurred in the Indo-Pacific *Opisthopterus*, in which the correspondence to the Gasteropelecid form is increased by the smooth ventral profile and the more posterior insertion of the dorsal, which in this genus commences behind the anal origin.



Shark, *Carcharhinus* sp., probably *C. leucas* (Müller & Henle), taken at "Rosaura" Station 41. A female specimen, total length 211 cm. (Photo J. S. Colman.)



Electric Rays, *Diplobatis pictus* Palmer. Two female specimens, actual size, from " Rosaura" Station 36. The outlines have been retouched. (Photo British Museum (Natural History).)

5. SPONGES

By MAURICE BURTON

With Plate 9 *and Text-figs.* 1–9

SYNOPSIS

The 42 specimens, representing 35 species, of which 8 are new, were collected from widely separated points on the Atlantic seaboards, providing useful fauna records. Two specimens are of special interest, since they make possible re-descriptions of species long known but too inadequately described to make recognition possible. The species are *Stryphnus pachastrelloides* (Schmidt) and *Callyspongia tenerrima* (Duchassaing and Michelotti).

I. LIST OF SPECIES MENTIONED IN THIS REPORT

Order HEXACTINELLIDA.

Sub-order AMPHIDISCOPHORA.

Family HYALONEMATIDAE.

Pheronema carpenteri (Thomson).

Sub-order HEXASTEROPHORA.

Family FARREIDAE.

Farrea occa Bowerbank.

Family MELETTIONIDAE.

Aphrocallistes beatrix Gray.

Family ROSSELLIDAE.

Rossella mortenseni Burton.

Order CALCAREA.

Family HOMOCOELIDAE.

Leucosolenia botryoides (Ellis and Solander).
Leucosolenia canariensis (Michlucho-Maclay).

Order TETRAXONIDA.

Sub-order STREPTASTROSCLEROPHORA.

Family THENEIDAE.

Thenea fenestrata (Schmidt).
Thenea wyvilli Sollas.

Sub-order ASTROSCLEROPHORA.

Family STELLETTIDAE.

Stelletta anancora (Sollas).
Stryphnus pachastrelloides (Schmidt).

Family CLAVULIDAE.

Radiella sol Schmidt.

Family TETILLIDAE.

Tetilla cranium (Müller).

Sub-order SIGMATOSCLEROPHORA.

Family HAPLOSCLERIDAE.

Haliclona rubens (Pallas).
,, *erina* de Laubenfels.
,, *spiculosa* (Dendy).
,, *calcinea* sp. n.
,, *tenerrima* sp. n.
Callyspongia tenerrima Duchassaing and Michelotti.

Family DESMACIDONIDAE.

Desmacella annexa (Schmidt).
,, *inornata* (Bowerbank).
Myxilla distorta sp. n.
Phorbas amaranthus (Duchassaing and Michelotti).
Inflatella viridis (Topsent).
Plocamionida topsenti sp. n.
Tedania anhelans (Lieberkühn).

Family AXINELLIDAE.

Axinella ramosa sp. n.
Hymeniacidon assimilis (Levinsen).
,, *glabrata* sp. n.
Halichondria panicea (Pallas).
,, *osculum* Lundbeck.
,, *bowerbanki* Burton.
,, *cornuloides* sp. n.

Family RASPELIIDAE.

Higginsia strigilata (Lamarck).
Dragmatyle topsenti sp. n.

Order KERATOSA.

Family SPONGIIDAE.

Hircinia variabilis Schmidt.

II. SYSTEMATIC NOTES

Order HEXACTINELLIDA.

Sub-order AMPHIDISCOPHORA.

Family HYALONEMATIDAE.

Genus *Pheronema* Leidy.

Pheronema carpenteri (Thomson).

Holtenia carpenteri Thomson, 1869, p. 120, woodcut; Thomson, 1869, p. 210; Thomson, 1869, p. 702, pls. lxvii–lxxi; *Pheronema carpenteri*, Kent, 1870, p. 243, pl. lxiii, fig. 1; Gray, 1870, p. 210; *Holtenia carpenteri*, Bocage, 1871, p. 69; *Pheronema carpenteri*, Marshall, 1876, p. 130; Schulze, 1886, p. 64; Schulze 1887, p. 241, pl. liii; Schulze, 1893, p. 562; Schulze, 1904, p. 50, pl. xv, figs. 1–5; Burton, 1928, p. 14.

OCCURRENCE. St. 49, between Fuerteventura Island (Canaries) and Africa (28° 25′ N., 13° 34′ W.), 1st February, 1938. One specimen.

DISTRIBUTION. Iceland; Faroes; Lewis; Portugal; Brazil; Zanzibar; 823–2928 m., on mud.

REMARKS. In spite of the wide geographical range, and the number of references to this species in the literature, it has not been recorded on more than five occasions. Yet from the numbers of individuals referred to in those references the species would appear to be abundant at suitable depths. This is borne out by the account Bocage (l.c.) gives. He refers to it as well-known to the " pêcheurs des squales " in the deep waters off Setubal.

In dealing with this species in 1928, I gave a reference to " Carpenter and Thomson 1869 " both in the synonymy list and in the list of literature. This was taken from Lendenfeld's bibliography in his work of 1886 (p. 598). There are two papers listed by Lendenfeld under this supposed joint authorship, both for the year 1869, and both were written, in fact, by Thomson alone.

Another correction is necessary, this time from Marshal (1876). This author lists the genus " *Holtenia* Schmidt " on p. 126, for *H. pourtalesii* and, on p. 130, gives " *Holtenia* Schmidt p.p. " under *Pheronema*. The only valid authorship of *Holtenia* is, of course, of Thomson, 1869.

Sub-order HEXASTEROPHORA

Family FARREIDAE

Genus *Farrea* Bowerbank

Farrea occa Bowerbank

(for discussion see Ijima, 1927)

OCCURRENCE. St. 49, between Fuerteventura Island (Canaries) and Africa (28° 25′ N., 13° 34′ W.), 1st February, 1938, 1300 m. One specimen.

DISTRIBUTION. World-wide, from 204–1901 m.

REMARKS. I find it difficult to believe that the many subspecies, into which Ijima divided this species, represent anything more than simple fluctuating variations, or, at most, ecological varieties.

Family MELETTIONIDAE

Genus *Aphrocallistes* Gray

Aphrocallistes beatrix Gray

Aphrocallistes beatrix Gray, 1858, p. 114, pl. xi; Ijima, 1927, p. 286, pl. xxiv, figs. 20–30, pl. xxv, figs. 1–25, text-fig. 35.

OCCURRENCE. St. 34, off St. George, Grenada, West Indies (12° 25′ N., 61° 49′ W.), 27th November, 1937, 720–800 m. One specimen.

DISTRIBUTION. South-west of Ireland; Azores; Madeira; Canaries; Cape Verde Islands; Ascension Island; Bermuda; Florida; West Indies; Indian Ocean (south of Bombay, Bay of Bengal, Andaman Islands); Malay Area; Philippines; Japan; 105–1633 m., on gravel, sand, mud and ooze.

Family ROSSELLIDAE

Genus *Rossella* Carter

Rossella mortenseni Burton

Rossella mortenseni Burton, 1928, p. 9, figs. 3–9.

OCCURRENCE. St. 49, between Fuerteventura Island (Canaries) and Africa (28° 25′ N., 13° 34′ W.), 1st February, 1938, 1300 m. One specimen.

DISTRIBUTION. Iceland; Faroes; 479–957 m.

Order CALCAREA

Family HOMOCOELIDAE

Genus *Leucosolenia* Bowerbank

Leucosolenia botryoides (Ellis & Solander)

Spongia botryoides Ellis and Solander, 1786, p. 190, pl. lviii, figs. 1–4; *Leucosolenia botryoides*, Arndt, 1939, p. 4, fig. 1.

OCCURRENCE. St. 10, NW. Arm, Horn Bay, Newfoundland (52° 13′ N., 55° 47′ W.), 23rd September, 1937, 15 m. One specimen.

DISTRIBUTION. Arctic; Atlantic coasts of Europe; Mediterranean; West Africa; South Africa; Red Sea; Australia (west and east coasts); Atlantic coast of North America; California; Chile; Sandwich Isles; mainly littoral, but occurring down to 860 m., growing on rocks, stones and seaweeds.

Leucosolenia canariensis (Michlucho-Maclay)

Nardoa canariensis Michlucho-Maclay, 1868, p. 230 ; *N. sulphurea* Michlucho-Maclay, 1868, p. 230 ; *N. rubra* Michlucho-Maclay, 1868, p. 230 ; *Tarroma canariense*, Haeckel, 1870, p. 244 ; *T. rubrum*, Haeckel, 1870, p. 245 ; *T. sulphureum*, Haeckel, 1870, p. 245 ; *Ascaltis canariensis*, Haeckel, 1872, p. 52, pl. ix, figs. 1–3, pl. x, fig. 1 ; *Auloplegma canariensis*, Haeckel, 1872, p. 52 ; *Ascuris arredifae* Haeckel, 1872, p. 52 ; *A. papillata* Haeckel, 1872, p. 52 ; *Ascetta compacta* Schuffner, 1877, p. 404, pl. xxv, fig. 9 ; *A. coriacea* var., Fristedt, 1885, p. 8 ; *Ascuris canariensis*, Lackschewitsch, 1886, p. 338 ; *Leucosolenia nausicae* Lackschewitsch, 1886, p. 300, pl. vii, fig. 1 ; *L. nanseni* Breitfuss, 1896, p. 427 ; Breitfuss, 1898, p. 106, pl. xii, figs. 1–9 ; Breitfuss, 1898, p. 13 ; *L. coriacea*, Arnesen, 1901, p. 10 ; Arnesen, 1901, p. 67 ; *L. canariensis* (pars), Thacker, 1908, p. 762, pl. xl. fig. 3, text-figs. 157–160 ; *Clathrina canariensis* var. *compacta* Row, 1909, p. 184 ; *Leucosolinia nanseni* Breitfuss, 1911, p. 311 ; *L. canariensis*, Dendy and Row, 1913, p. 724 ; *L. nanseni*, Derjugin, 1915, p. 289 ; *L. canariensis*, Hentschel, 1916, p. 4 ; Hozawa, 1918, p. 528, pl. lxxxiv, fig. 2 ; Breitfuss, 1932, p. 240 ; Hozawa, 1933, p. 2, pl. i, fig. 1 ; Topsent, 1934, p. 7.

OCCURRENCE. St. 10, NW. Arm, Horn Bay, Newfoundland (52° 13′ N., 55° 47′ W.), 23rd September, 1937, 15 m. Two specimens.

DISTRIBUTION. Spitzbergen ; Kola Fiord ; Norway ; Sweden ; Mediterranean ; Canaries ; Cape Verde Islands ; Mauritius ; Suez ; Japan ; on rock, sand, stones, mud, shells ; littoral to 165 m.

REMARKS. The similarity between the external form of this species and that of the better-known *L. coriacea* tempts the suggestion that it is a recurrent mutant of the latter. Both occupy a similar range, have the same colour varieties and a closely similar external form. If, as we have reason to believe, the presence or absence of oxea in calcareous sponges has no specific value, then the affinity between *L. canariensis* and *L. coriacea* is even closer, and the recognition of the former as a mutant of the latter depends mainly on the presence of quadriradiates.

Order TETRAXONIDA

Sub-order STREPTASTROSCLEROPHORA

Family THENEIDAE

Genus *Thenea* Gray

Thenea fesestrata (Schmidt)

Tisiphonia fenestrata Schmidt, 1880, p. 71, pl. x, fig. 2 ; *Thenea fenestrata*, Sollas, 1886, p. 185 ; *T. wrightii* Sollas, 1886, p. 185 ; Sollas, 1888, p. 63, pl. viii, figs. 11–20 ; *T. fenestrata*, Sollas, 1888, p. 71, pl. viii, figs. 1–8 ; *Ancorina* (*Thenea*) *fenestrata*, Lendenfeld, 1903, p. 55 ; *A.* (*T.*) *wrightii*, Lendenfeld, 1903, p. 58 ; *T. fenestrata*, Wilson, 1904, p. 88, pl. xiii, figs. 2–4, 6–7, 9 ; *T. echinata* Wilson, 1904, p. 91, pl. xii, figs. 1–9 ; *T. lamelliformis* Wilson, 1904, p. 95, pl. xii, figs. 10–13, pl. xiii, fig. 1.

OCCURRENCE. St. 26, north of Turneffe Island, West Indies (17° 53′ N., 84° 44′ W.), 7th November, 1937, 900 m. One specimen.

DISTRIBUTION. Galapagos ; Chile ; West Indies ; Sierra Leone ; 1745–4114 m., on mud and ooze.

Thenea wyvillii Sollas

Thenea wyvillii Sollas, 1886, p. 184; Sollas, 1888, p. 74, pl. vi, figs. 1–9; *T. calyx* Thiele, 1898, p. 24, pl. v, figs. 9–10; *Ancorina* (*Thenea*) *wyvillii*, Lendenfeld, 1903, p. 56; *A.* (*T.*) *grayi calyx*, Lendenfeld, 1903, p. 57.

OCCURRENCE. St. 49, between Fuerteventura Island and Africa (28° 25′ N., 13° 34′ W.), 1st February, 1938, 1300 m. One specimen.

DISTRIBUTION. Off Zebu, Philippines, 174 m., on blue mud.

REMARKS. The species evidently ranges throughout tropical waters. In addition to the present specimen from the tropical Atlantic and the holotype from the Philippines, there is a third specimen in the John Murray Collection, in the British Museum, from the Gulf of Aden.

Sub-order ASTROSCLEROPHORA

Family STELLETTIDAE

Genus *Stelletta* Schmidt

Stelletta anancora (Sollas)

Pilochrota anancora Sollas, 1886, p. 189; *P. gigas* Sollas, 1886, p. 190; *P. tenuispicula* Sollas, 1886, p. 190; *P. crassispicula* Sollas, 1886, p. 190; *P. gigas* Sollas, 1888, p. 124, pl. xx, figs. 1–13; *P. tenuispicula* Sollas, 1888, p. 127, pl. xv, figs. 28–32; *P. crassispicula* Sollas, 1888, p. 128, pl. xiv, figs. 9–15; *P. anancora* Sollas, 1888, p. 132, pl. xiv, figs. 16–22; *Stelletta crassispicula*, Lendenfeld, 1903, p. 42; *S. tenuispicula*, Lendenfeld, 1903, p. 42; *S. anancora*, Lendenfeld, 1903, p. 43; *S. gigas*, Lendenfeld, 1903, p. 43; *S. crassiclada* Lendenfeld, 1906, p. 281, pl. xxxi, figs. 3–12; *S. crassispicula*, Topsent, 1922, p. 1; Topsent, 1928, p. 123, pl. i, fig. 25, pl. v, fig. 13.

OCCURRENCE. St. 44, St. Paul's Rock, 28th December, 1937, 50–60 m. One specimen.

DISTRIBUTION. Bermuda; Cape Verde Islands; St. Paul's Rock; Bahia; on rock and calcareous algae; 12–91 m.

REMARKS. Topsent (1922) has given an account of the variations in this species, and on the basis of this has suggested the identity of *S. crassiclada* and *S. crassispicula*. It is difficult to understand why he failed at the same time to recognize Sollas' *Pilochrota anancora*, *P. gigas* and *P. tenuispicula* as synonyms also; the species name is, by priority, *Stelletta anancora*.

Genus *Stryphnus* Sollas

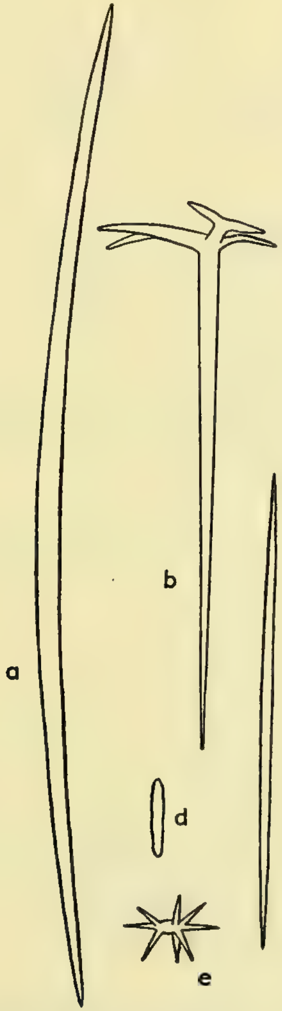
Stryphnus pachastrelloides (Schmidt)

(Text-fig. 1)

Ancorina pachastrelloides Schmidt, 1870, p. 68; Sollas, 1888, p. 205; Lendenfeld, 1903, p. 66.

OCCURRENCE. St. 49, between Fuerteventura Island and Africa (28° 25′ N., 13° 34′ W.), 1300 m., 1st February, 1938. One specimen.

REMARKS. Schmidt's original description of this species, alone, was inadequate for purposes of identification. With the few details he gives, together with a poor spicule preparation made by him and now in the British Museum (Reg. No. 70.5.3.48), it is possible to recognize the species when these two things can be compared with fresh material. The present specimen, although collected in the eastern Atlantic, whereas the holotype was taken off Florida, is massive, with a



TEXT-FIG 1. *Stryphnus pachastrelloides* (Schmidt). *a*, oxeote, × 50; *b*, dichotriaene, × 50; *c*, microxeote, × 500; *d*, microstrongyle, × 500; *e*, amphiaster, × 500.

cylindrical outgrowth. There is one oscule at the summit of the main mass and one at the end of the outgrowth, each leading into a deep cloaca. The colour, in spirit, is a pale yellowish-brown. Schmidt described the sponge as " unregelmässige Knollen mit unregelmässig cylindrischen Fortsätzen." The only other guide to the external appearance is given : " Die Rindenschicht wird lediglich durch . . . ein bräunliches Pigment vertreten." The skeleton of the " Rosaura " specimen consists of large radially-arranged oxea, short-shafted dichotriaenes, with microxea, roughened microstrongyla and amphiasters. There appear to be present, also, oxyasters, but these, I believe, are no more than the amphiasters seen in end-view. The spicule-preparation (70.5.3.48) contains these same categories, and they are of similar dimensions in each case. There are, however, a number of smooth strongyla, about the same length as the microxea but much thicker. At first sight, the strongyla seem proper to the sponge but the discovery of a number of other more obviously extraneous spicules in this preparation suggests that the strongyla may also be foreign to it. Schmidt's preparations, of which the British Museum has many, are notorious for either the poverty of their proper spicules or the richness of those spicules accidentally included. The identity of Schmidt's holotype, based on B.M. 70.5.3.48, and the present specimen is made the more certain by the presence, in both, of a faint annulus at the centre of so many of the microxea.

The species may be re-described :

Irregularly massive with cylindrical outgrowths ; surface uneven, hispid ; oscules large, apical ; texture firm, incompressible ; colour, in spirit, light brown ; skeleton of radially-arranged oxea and short-shafted dichotriaenes, with microxea, microstrongyla and amphiasters for microscleres :

Spicules : Oxea, slightly curved, 3·2 by 0·06 mm., dichotriaenes, cladome 0·6 mm. across, rhabdome 1·5 by 0·048 mm., microxea, 0·14 by 0·004 mm., microstrongyla 0·024 by 0·004 mm., amphiasters 0·028 mm. across.

Family CLAVULIDAE

Genus *Radiella* Schmidt

Radiella sol Schmidt

Trichostemma hemisphaericum Sars, 1869, p. 259 [nom. nud.] ; *Radiella sol* Schmidt, 1870, p. 48, pl. iv, fig. 6 ; *Trichostemma hemisphaericum* Sars, 1872, p. 62, pl. vi, figs. 1–15 ; *Radiella sol*, Burton, 1930, p. 510 ; Burton, 1934, p. 15.

Occurrence. St. 26, north of Turneffe Island, West Indies (17° 53′ N., 87° 44′ W.), 900 m. One specimen.

Distribution. Greenland ; between Norway and Bear Island ; Barents Sea ; Kara Sea ; Franz Josef Land ; Norway (Lofoten) ; West Indies ; 97–1167 m., on clay and mud.

Family TETILLIDAE

Genus *Tetilla* Schmidt

Tetilla cranium (Müller)

Alcyonium cranium Müller, 1776, p. 255 ; *Tethya cranium*, Lamarck, 1815, p. 71 ; *Craniella cranium*, Sollas, 1888, p. 51 ; *Tethya cranium*, Topsent, 1913, p. 12, pl. iii, fig. 3, pl. v, fig. 12.

OCCURRENCE. St. 34, off St. George, Grenada, West Indies (12° 25′ N., 61° 49′), 27th November, 1937, 720–800 m. One specimen.

DISTRIBUTION. Arctic; Atlantic coast of Europe; Azores; West Indies; Ceylon; Japan; Pacific coast of North America; 9–1829 m., on rock, gravel, sand, mud and ooze.

Family HAPLOSCLERIDAE

Genus *Haliclona* Grant

Haliclona rubens (Pallas)

Spongia rubens Pallas, 1766, p. 389; Duchassaing and Michelotti, 1864, p. 41, pl. x, fig. 1 ; *Pachychalina rubens*, Schmidt, 1870, p. 37 ; *Chalina rubens*, Carter, 1882, p. 276; *Chalinopsis rubens*, Lendenfeld, 1887, p. 744 ; *Ceraochalina rubiginosa* Lendenfeld 1887, p. 779 ; *Pachychalina rubens*, Wilson, 1902, p. 392 ; *Cladochalina rubens*, Burton, 1927, p. 511 ; *Haliclona rubens*, de Laubenfels, 1932, p. 59 ; 1936, p. 42, pl. vii, fig. 2, pl. viii, fig. 1 ; de Laubenfels, 1949, p. 9.

OCCURRENCE. St. 31, Gorda Cay, Mosquito Bank, West Indies (15° 54′ N., 82° 13′ W.), 16th November, 1937, 34 m. One specimen.

DISTRIBUTION. Dry Tortugas; Bahamas; Long Key Island; Guadeloupe; Viecques; St. Domingo; St. Thomas; Cuba; Porto Rico; 1–17 m.

Haliclona erina de Laubenfels

Haliclona erina de Laubenfels, 1936, p. 457.

OCCURRENCE. St. 10, NW. Arm, Horn Bay, Newfoundland (52° 13′ N., 55° 47′ W.), 23rd September, 1937, 15 m. Two specimens.

DISTRIBUTION. Panama (Caribbean).

REMARKS. These specimens, although agreeing with the holotype in structure and appearance, were obtained well away from the type locality. It is therefore worth recalling de Laubenfels' comment, in describing the species: " It must be admitted that this may be a remarkable modification of some previously described *Haliclona*, due perhaps to unusual environment conditions, but it is impossible to say which *Haliclona* has been so modified." This expresses the situation for so many specimens of *Haliclona* from all parts of the world.

Haliclona spiculosa (Dendy)

Siphonochalina spiculosa Dendy, 1887, p. 505; Dendy, 1890, p. 354, pl. lviii, fig. 2, pl. lxii, fig. 3; Wilson, 1902, p. 394.

OCCURRENCE. St. 24, Turneffe Island, West Indies (17° 15′ N., 87° 49′ W.), 1st November, 1937, 2 m. One specimen.

DISTRIBUTION. Turk's Island, Bahamas; St. Thomas; 2–42 m.

REMARKS. The species is doubtfully referred to the genus *Haliclona*, principally on the absence of a special tangential skeleton at the surface.

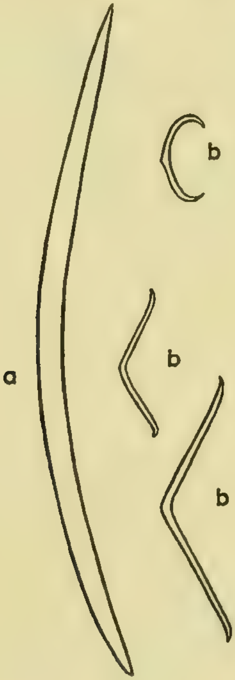
Haliclona calcinea sp. n.

(Pl. 9, fig. 1; Text-fig. 2)

HOLOTYPE. B.M. 1938.6.30.31.

OCCURRENCE. St. 34, off St. George, Grenada, West Indies (12° 25′ N., 61° 49′ W.), 27th October, 1937, 720–800 m. One specimen.

DESCRIPTION. Sponge massive, rounded; surface even, minutely hispid; oscules small, scattered; texture firm, friable; colour, in spirit, dark brown; skeleton subhalichondroid, mainly unispicular; megascleres oxea, 0·5 by 0·016 mm.,



TEXT-FIG. 2. *Haliclona calcinea* sp. n. *a*, oxeote, × 200; *b*, toxa and sigma, × 500.

microscleres centrangulated sigmata, 0·024 mm. chord, and toxa, 0·04 to 0·08 mm. chord.

REMARKS. Although the colour is given as dark brown, this applies strictly to the ectosome, whether of the outer surface or of the linings of the large canals. The choanosome is a dull brownish-yellow. The surface, moreover, is largely coated with a pale greyish yellow, in places up to 3 mm. thick. This apparent incrustation has the same spicules as the main body and must be presumed to represent new growth.

The species differs, in its external form, as well as in the detailed measurements of the microsclercs, from other species of *Haliclona* having such long oxea combined with the presence of microscleres.

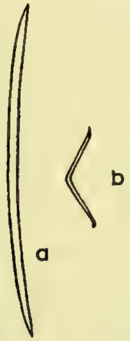
Haliclona tenerrima sp. n.

(Pl. 9, fig. 2; Text-fig. 3)

HOLOTYPE. B.M. 1938.6.30.42.

OCCURRENCE. St. 24, Turneffe Island, British Honduras (17° 16′ N., 87° 50′ W.), 1st November, 1937, 3½ m. One specimen.

DESCRIPTION. Sponge a fragment only; surface uneven, minutely hispid; oscules not present; texture soft, compressible, elastic; colour, in spirit, pale yellow; skeleton irregularly sub-isodictyal (almost halichondroid) with triangular mesh, and with occasional fibres of 2 to 3 spicules width running to surface; megascleres oxea, 0·28 by 0·007 mm.; microscleres toxa, 0·03 to 0·1 mm. chord.



TEXT-FIG. 3. *Haliclona tenerrima* sp. n. *a*, oxeote, × 200; *b*, toxon, × 500.

Callyspongia tenerrima Duchassaing & Michelotti

Calyspongia tenerrima Duchassaing & Michelotti, 1864, p. 57, pl. x, figs. 3–4.

OCCURRENCE. St. 31, Gorda Cay, Mosquito Bank, West Indies (15° 54′ N., 82° 13′ W.), 16th November, 1937, 34 m. One specimen.

DISTRIBUTION. West Indies (St. Thomas, Viecques).

Diagnosis. Sponge branching, stipitate, slender, dichotomous; surface even; oscules small, in linear series along branches; texture soft, compressible; colour, in life and in spirit, yellow tinted with rose; main skeleton an irregular network of mainly quadrangular mesh, with recognizable primary, secondary and tertiary fibres; special ectosomal skeleton, of similar structure but with meshes mainly triangular; fibres 0·03 to 0·08 mm. diameter, cored by 1-4 spicules; megascleres strongyla, 0·1 by 0·002 to 0·003 mm.; microscleres absent.

Remarks. The holotype has been lost, as was ascertained some years ago by de Laubenfels during his visit to Turin. The original description, inadequate though it is, leaves, no doubt of the identity of the present specimen. The holotype was described as " phytoide, dichotome, grêle . . . les rameaux . . . cylindriques . . . jaune un peu rosè " in life with small oscules in series along the branches. Every one of these features is found in the present specimen. Above all, the peculiar appearance of the surface, shown in fig. 4 (Duchassaing & Michelotti, l.c.) puts the identification beyond reasonable doubt.

Family DESMACIDONIDAE

Section Mycaleae

Genus *Desmacella* Schmidt

Desmacella annexa (Schmidt)

Desmacella annexa Schmidt, 1870, p. 53; *Tylodesma annexa*, Burton, 1930, p. 525.

Occurrence. St. 34, off St. George, Grenada, West Indies (12° 25′ N., 61° 49′ W.), 27th November, 1937, 720–800. Two specimens.

Distribution. Iceland; Norway; south-west Ireland; Atlantic coast of France; Mediterranean; West Indies; Florida; Indian Ocean; 85–1331 m., on rock, mud and ooze.

Desmacella inornata (Bowerbank)

Halichondria inornata Bowerbank, 1866, p. 271; *Tylodesma inornata*, Burton, 1930, p. 527.

Occurrence. St. 34, off St. George, Grenada, West Indies (12° 25′ N., 61° 44′ W.), 27th November, 1937, 420–800 m. One specimen.

Distribution. British Isles; France; Spain; Mediterranean; Azores; 200–1025 m., on mud, sand, gravel, broken shells, rocks.

Section Myxilleae

Genus *Myxilla* Schmidt

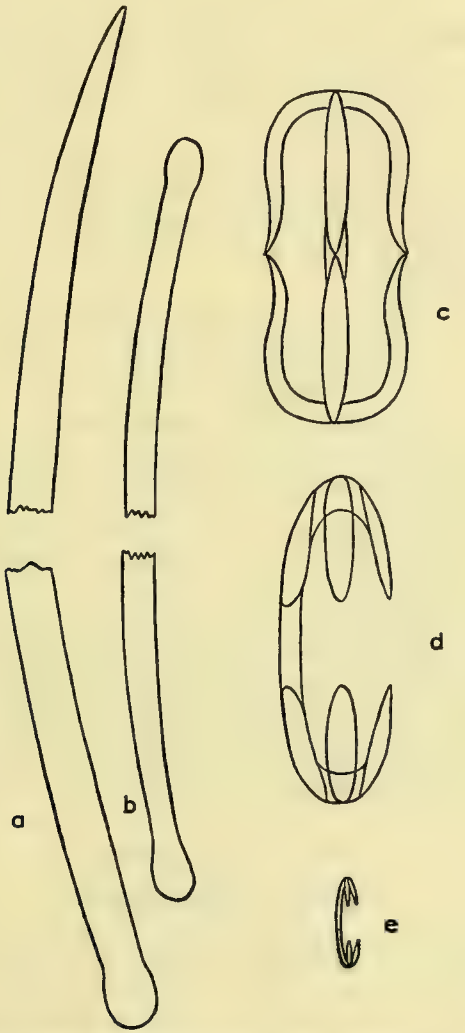
Myxilla distorta sp. n.

(Pl. 9, fig. 3, Text-fig. 4)

Holotype. 1938.6.30.30.

Occurrence. St. 34, off St. George, Grenada, West Indies (12° 25′ N., 61° 49′ W.), 27th November, 1937, 720–800 m. One specimen.

Description. Sponge erect, lobate; surface uneven; harsh to touch; oscules at apices of lobes; texture firm, incompressible, friable; colour, in spirit, pale yellow; main skeleton an irregular reticulation of bluntly-pointed curved styli, 1·0 by 0·024 mm.; ectosomal skeleton a tangential reticulation of irregular mesh formed of tornota with both ends tylote and measuring 0·72 by 0·016 mm.; micro-



Text-fig. 4. *Myxilla distorta* sp. n. *a*, style, × 300; *b*, tornote, × 300; *c*, isochela with teeth meeting in middle line (front view), × 600; *d*, normal large isochela, × 600; *e*, small isochela, × 600.

scleres isochelae spatuliferae, larger frequently distorted by unusual length of teeth, ranging from 0·024 to 0·08 mm. chord.

REMARKS. The species is peculiar in the presence of the distorted chelae, but is also separable from other known species in the remaining details of its spiculation.

Genus *Phorbas* Duchassaing & Michelotti

Phorbas amaranthus Duchassaing & Michelotti

Phorbas amaranthus Duchassaing & Michelotti, 1864, p. 92, pl. xxi, fig. 1; *Cribrella hospitalis* Schmidt, 1870, p. 56, pl. iv, fig. 12; ? *Anchinoë fictitius*, Topsent, 1928, p. 284; *Phorbas amaranthus*, de Laubenfels, 1936, p. 63.

OCCURRENCE. St. 31, off Gorda Bay, Mosquito Bank, West Indies (15° 54′ N., 82° 13′ W.), 16th November, 1937, 34 m. One specimen.

DISTRIBUTION. Florida; West Indies; ? Azores; ?? Morocco and Spain; 27 m.

REMARKS. Since this species has never been adequately described, a description based on the holotype is given:

Sponge encrusting or massive and irregularly digitate; surface villous, particularly in larger individuals; oscules not apparent; pores in sieves; texture firm; colour, alive, maroon, in spirit, almost white; skeleton of ascending fibres of serially-arranged tornota, echinated by acanthostyli of two sizes, and with a tangential ectosomal layer of tornota similar to those of main skeleton; tornota, with oxeate to hastate ends, 0·2 to 0·36 by 0·004 to 0·005 mm.; large acanthostyli, 0·2 by 0·006 mm., small acanthostyli, 0·1 by 0·006 mm., microscleres isochelae arcuatae, 0·026 mm. chord.

In a very brief redescription of the species, de Laubenfels (1936) describes the microscleres as chelae and rare sigmata. I have found no sigmata in my preparations from the type.

Topsent (1928) records specimens of *Achinoë fictitius*, from the Azores, Morocco and Spain, having a spiculation similar to that of *Phorbas amaranthus*. In addition, he includes *Cribrella hospitalis* Schmidt as a synonym of his supposed *Anchinoë fictitius*, but Schmidt's species is identical with *Phorbas amaranthus*. Whether, indeed, this West Indian species extends to the Azores is problematic, but it is highly doubtful that it should also occur off Morocco and Santander. Re-examination of Topsent's material is needed to settle this.

Genus *Inflatella* Schmidt

Inflatella viridis (Topsent)

Joyeuxia viridis Topsent, 1890, p. 29; Topsent, 1892, p. 94, pl. ii, fig. 8, pl. x, fig. 19; *Inflatella viridis*, Lundbeck, 1910, p. 20, pl. ii, figs. 11–12, pl. iv, fig. 7; Hentschel, 1929, p. 968; *nec* Topsent, 1904, p. 205.

OCCURRENCE. St. 34, St. George, Grenada, West Indies (12° 05′ N., 61° 49′ W.), 27th November, 1937, 720–800 m. One specimen.

DISTRIBUTION. Denmark Strait; Azores; 136–1768 m.

Genus *Plocamionida* Topsent

Plocamionida topsenti sp. n.

(Text-fig. 5)

Holotype. 1938.6.3.29.

Occurrence. St. 34, off St. George, Grenada, West Indies (12° 25′ N., 61° 49′ W.), 27th November, 1937, 720–800 m. One specimen.

Description. Sponge thinly encrusting; surface hispid; oscules not apparent; colour, in spirit, pale greyish-yellow; skeleton of styli, 1·2 by 0·04 mm., and acanthostyli, 0·24 by 0·008 mm., with occasional intermediates; ectosomal tornota, with ends strongylote or faintly subtylote, 0·36 by 0·006 mm., acanthostrongyla, 0·18 by 0·014 mm.; microscleres isochelae arcuatae, 0·06 to 0·068 mm. chord.

Remarks. The species differs from all others in the genus in the much larger sochelae, as well as in other details of the spiculation.

Section Tedanieae

Genus *Tedania* Schmidt

Tedania anhelans (Lieberkühn)

Halichondria anhelans Lieberkühn, 1859, p. 521, pl. xi, fig. 6; *Tedania nigrescens*, Burton, 1932, p. 346, fig. 44; *Xytopsibis asperus* de Laubenfels, 1936, p. 61.

Occurrence. St. 24, Turneffe Island (17° 15′ N., 87° 49′ W.), 1st November, 1937, 2 m. One specimen.

Distribution. Mediterranean; Cape Verde Islands; Bermuda; West Indies; West Africa; Red Sea; Indian Ocean; Indonesia; Cochin-China; Australia; littoral to 120 m., on rock, stones, shells, mud or sand.

Remarks. The species has been fully discussed (Burton, 1932) under *Tedaria nigrescens* (Schmidt). This name is, however, pre-empted by *Halichondria anhelens* Liebekühn which, as shown by the original description and by Schmidt's (1862, p. 74) finding of tornota in preparations of the type, is identical with the widespread species known so long under Schmidt's name.

Family AXINELLIDAE

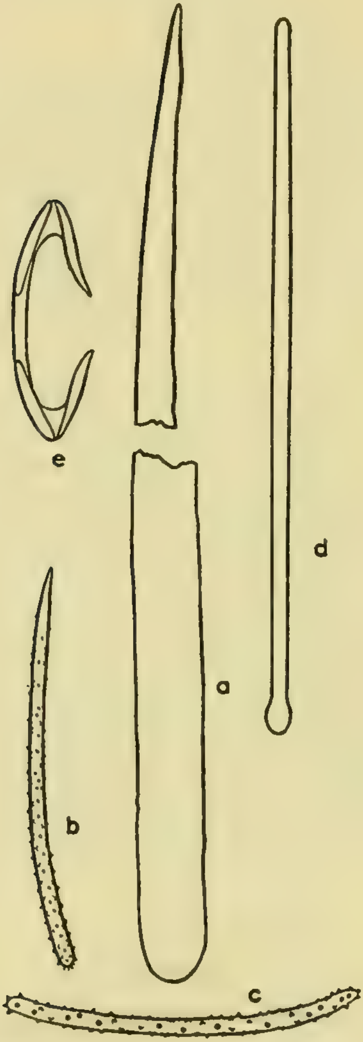
Genus *Axinella* Schmidt

Axinella ramosa sp. n.

(Pl. 9, fig. 4; Text-fig. 6)

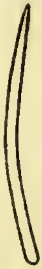
Holotype. 1938.6.30.37.

Occurrence. St. 31, off Gorda Bay, Mosquito Bank, West Indies (15° 54′ N., 82° 13′ W.), 16th November 1937. Three specimens.



TEXT-FIG. 5. *Plocamionida topsenti* sp. n. *a*, style, × 300 · *b*, acanthostyle, × 300; *c*, acanthostrongyle, × 300; *d*, tornote, × 300; *e*, isochela, × 600.

DESCRIPTION. Sponge branching; surface slightly uneven, minutely hispid; oscules not apparent; texture firm; colour, in spirit, pale yellow; skeleton subisodictyal, ascending fibres somewhat plumose, connectives mainly unispicular; megascleres styli, 0·4 by 0·016 mm.; microscleres absent.



TEXT-FIG. 6. *Axinella ramosa*, sp. n. *a*, style, × 100.

REMARKS. There are three specimens, the largest, the holotype, is 65 mm. high with its branches 4 mm. in diameter at most. The other two are considerably smaller.

Genus *Hymeniacidon* Bowerbank

Hymeniacidon assimilis (Levinsen)

Halichondria assimilis Levinsen, 1886, p. 352, pl. xxx, fig. 5; *Hymeniacidon assimilis*, Burton, 1935, p. 74.

OCCURRENCE. St. 5, Julianshaab, Greenland (60° 43′ N., 46° 02′ W.), 4th September, 1937, 80 m. One specimen.

DISTRIBUTION. Kara Sea; Sea of Japan; Sea of Okhotsk; littoral to 124 m., on seaweeds.

Hymeniacidon glabrata sp. n.

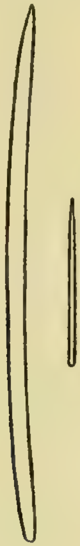
(Pl. 9, fig. 5; Text-fig. 7)

HOLOTYPE. 1938.6.30.35.

OCCURRENCE. St. 22, Belize Harbour, West Indies (17° 28′ N., 88° 11′ W.), 29th October, 1937, 6 m. One specimen.

DESCRIPTION. Sponge encrusting, agglutinating; surface even, minutely hispid; oscules at ends of cloacae running parallel to and just under surface; texture soft, compressible; colour, in spirit, pale greyish-yellow; main skeleton halichondroid, with tendency to multispicular ascending fibres; ectosomal skeleton a loose network of more or less quadrangular mesh; megascleres styli, thickest at centre (? incompletely differentiated into two sizes), ranging from 0·24 to 0·8 by 0·004 to 0·024 mm.

REMARKS. The holotype is a thin and flattened, somewhat irregular plate, with a number of small bivalve shells incorporated in its lower surface. Being no more than a fragment, the interpretation of its mode of growth is difficult. In general appearance it recalls *H. tubulosa* (Ridley & Dendy) from the mouth of the River Plate, which has, presumably, a more erect growth ; and also larger spicules.



TEXT-FIG. 7. *Axinella glabrata* sp. n. Large and small styli, × 100.

Genus *Halichondria* Fleming

Halichondria panicea (Pallas)

Spongia panicea Pallas, 1766, p. 388 ; *Halichondria panicea*, Arndt, 1928, p. 52.

OCCURRENCE. St. 1, Angmagssalik Harbour, Greenland (65° 35′ N., 37° 20′ W.), 27th August, 1937, 25–50 m. One specimen.

DISTRIBUTION. Arctic ; Atlantic coasts of Europe (including Baltic Sea) ; Mediterranean ; Black Sea ; Atlantic coast of Africa to Saldanha Bay ; St. Paul ; Patagonia ; Chile ; Atlantic coasts of North America, south to Newfoundland ; Pacific coast of Asia, south to Japan ; Indian Ocean (Ceylon) ; Kerguelen ; New Zealand ; littoral to 183 m.

Halichondria tenera (Marenzeller)

Isodictya tenera Marenzeller, 1877, p. 364, pl. i, fig. 2 ; Burton, 1930, p. 516 ; *Halichondria tenera*, Burton, 1935, p. 76.

OCCURRENCE. St. 1, Angmagssalik Harbour, Greenland (65° 35′ N., 37° 20′ W.), 27th August, 1937, 25–50 m. One specimen.

Distribution. Franz Josef Land; Sea of Japan; Sea of Okhotsk; 2–178 m., mud.

Remarks. This sponge, which is massive, or may be massively branched, with uneven surface, small scattered oscules and a soft friable texture, has for main skeleton a loose isodictyal reticulation. The tangential ectosomal skeleton is ill-developed; the sole spicules are oxea 0·3 to 0·4 by 0·003 to 0·01 mm. The species is not, therefore, a typical *Halichondria*. It may even have affinities with the species of *Adocia*, except that the oxea are more like those typical for *Halichondria*.

Halichondria osculum Lundbeck

Halichondria osculum Lundbeck, 1902, p. 23, pl. iii, figs. 3–7, pl. ix, figs. 7–9; Hentschel, 1929, p. 991.

Occurrence. St. 10, NW. Arm, Horn Bay, Newfoundland (52° 13′ N., 55° 47′ W.), 23rd September, 1937, 15 m. One specimen.

Distribution. Greenland, 18–718 m.

Remarks. The specimen forms a small irregular mass, 10 mm. across, growing on a Nullipore. There is an encrusting body with processes arising from it and it is these which determine its identification with Lundbeck's species. Although much smaller than Lundbeck's original specimens, each process bears a strong resemblance to them. On the other hand, the spicules are somewhat smaller, none exceeding 0·6 mm., or slightly more, by 0·012 mm., against a maximum of 0·7 by 0·17 mm., in the types.

On first examination I had taken this to be the type of a new species, but on further consideration accept it as an atypical specimen of *Halichondria osculum*.

Halichondria bowerbanki Burton

Spongia coalita Lamouroux, 1816, p. 80; *Halichondria coalita*, Topsent, 1911, pp. i–xv; *H. bowerbanki* Burton, 1930, p. 489.

Occurrence. St. 10, NW. Arm, Horn Bay, Newfoundland (17° 53′ N., 87° 44′ W.), 23rd November, 1937, 15 m. One specimen.

Remarks. *Halichondria bowerbanki* and *H. panicea* resemble each other closely in spiculation and in external appearance. In addition, both are extremely variable in form. The consequence is that, although Topsent (1911) has shown marked differences in their larvae, it is rarely possible to be certain of the identification of a given specimen. The present sample is of a loose-textured, massive sponge, about 100 mm. across and some 50 mm. high. Its surface is covered with low digitate processes, 3 to 4 mm. high. The identification given here is based on the translucent appearance and the fact that specimens having the cavernous quality of the inner tissues as well as the digitate processes of the surface have been collected by me off the coast of Devon. Even so, it is given with hesitation.

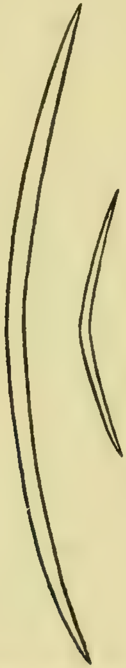
Halichondria cornuloides sp. n.

(Pl. 9, fig. 6; Text-fig. 8)

Holotype. B.M. 1938.6.30.41.

Occurrence. St. 1, Angmagssalik Harbour, Greenland (65° 35′, 37° 20′ W.), 27th August, 1937, 25–50 m. One specimen.

Description. Sponge irregularly massive, lobular; surface smooth, even, translucent; oscules (and pores ?) in circular cribriform areas at summits of low secondary lobes or apical on main lobes; texture firm, compressible owing to cavernous structure of inner tissues; colour, in spirit, yellowish; megascleres oxea, 0·2 to 0·5 by 0·008 to 0·012 mm.; microscleres absent.



Text-fig. 8. *Halichondria cornuloides* sp. n. Oxea, × 200.

Remarks. The species resembles in external appearance the various forms included by Dendy in his family Coelosphaeridae, and especially those of the genus *Cornulum*. So strong is this resemblance that I found it difficult to be convinced that it is a true *Halichondria*. Nevertheless, the oxea have the typical form and variable length, and the structure of both main and tangential ectosomal skeletons leave little doubt that it is a *Halichondria*.

Family RASPAILIIDAE

Genus *Higginsia* Higgin

Higginsia strigilata (Lamarck)

Spongia strigilata Lamarck, 1813, p. 450; Lamarck, 1816, p. 377; *Higginsia coralloides* Higgin, 1877, p. 291, pl. xiv, figs. 1–5.

Occurrence. St. 31, off Gorda Bay, Mosquito Bank, West Indies (15° 54′ N., 82° 13′ W.), 16th November, 1937, 34 m. One specimen.

Distribution. Ireland; west coast of Africa; West Indies; Natal; Amboina; Australia; littoral (?) to 20 m., on rock or coral rock.

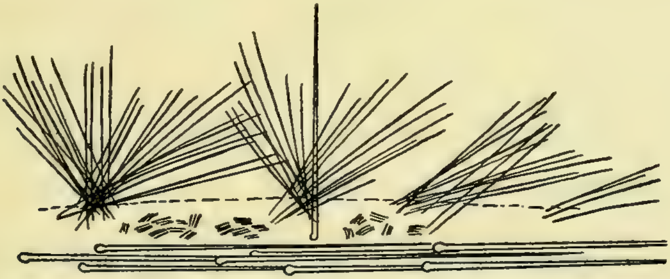
Remarks. Topsent (1933, p. 112) has shown that Higgin's *Higginsia coralloides* is the same as Lamarck's *Spongia strigilata*.

Genus *Dragmatyle* Topsent

Dragmatyle topsenti sp. n.

(Pl. 9, fig. 7; Text-fig. 9)

Occurrence. St. 26, north of Turneffe Islands, West Indies (17° 53′ N., 84° 44′ W.), 7th November, 1937, 900 m. Several fragments (belonging to one specimen ?)



Text-fig. 9. *Dragmatyle topsenti* sp. n. Section at right angles to surface, showing axial core of tylostyli; surface brushes of styloids, with occasional tylostyli set at right angles to surface; and trichodragmata.

Description. Sponge comprising slender branches; surface uneven, hirsute; oscules not apparent; texture soft, compressible; colour, in spirit, light brown; skeleton an axial core of tylostyli, with occasional tylostyli set at right angles and projecting beyond surface, with ectosomal brushes of oxeote styloids and trichodragmata for microscleres; tylostyli 1·6 by 0·014 mm., styloids 1·2 by 0·008 mm. trichodragmata, 0·06 mm. long.

Order KERATOSA

Genus *Hircinia* Nardo

Hircinia variabilis Schmidt

Hircinia variabilis Schmidt, 1862, p. 34, pl. iii, fig. 17; Lendenfeld, 1889, p. 557, pl. xxxvi, figs. 11–14.

OCCURRENCE. St. 31, off Gorda Cay, Mosquito Bank, West Indies (15° 54′ N., 37° 20′ W.), 16th November, 1937, 34 m. One specimen.

DISTRIBUTION. Mediterranean; West Indies and Florida; Indian Ocean; Australia; "Pacific Oceanic Islands"; 6–75 m.

REMARKS. If it be possible to recognize varieties in this extremely variable species, then the present specimen should be assigned to var. *dendroides*.

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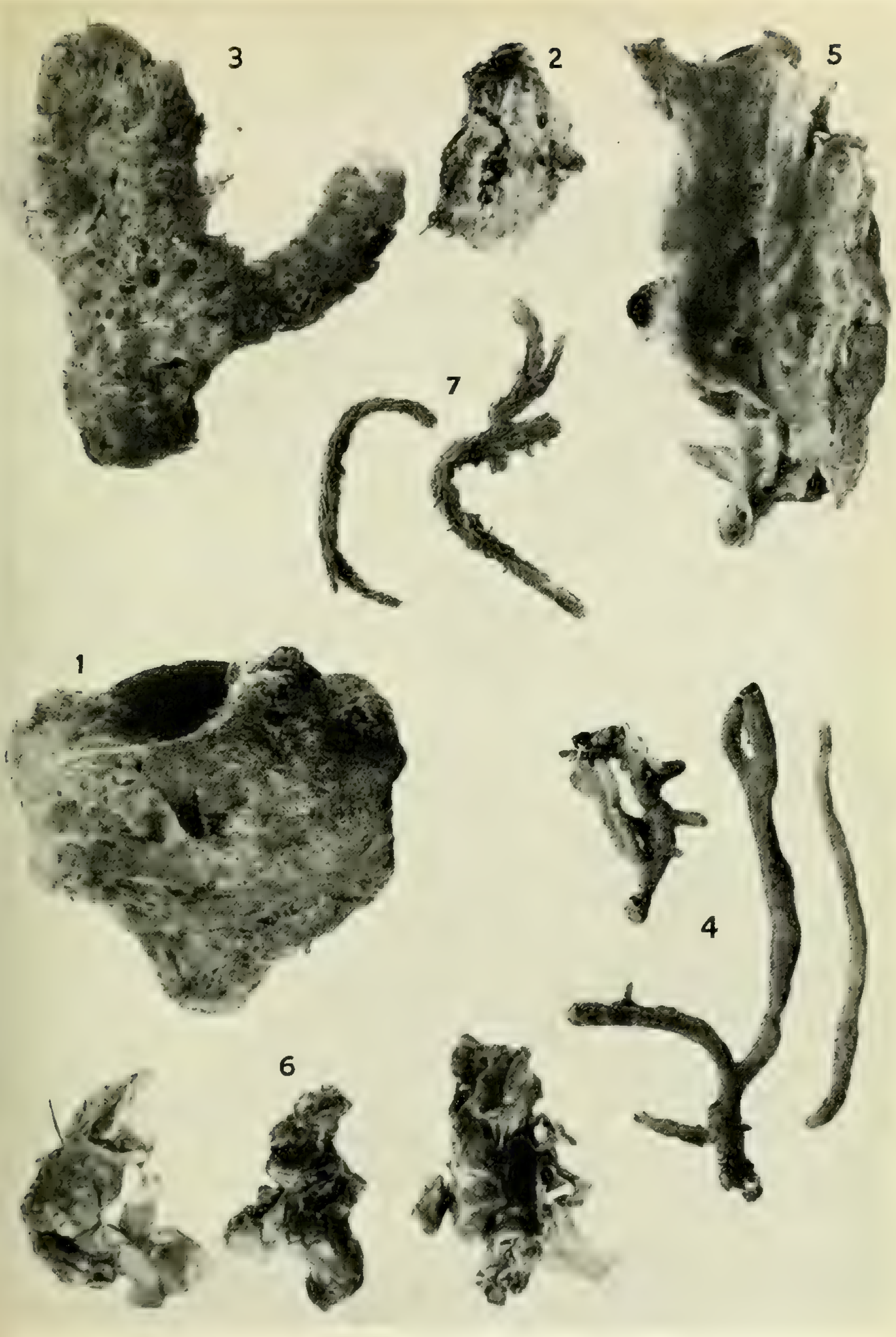
PRESENTED

PLATE 9

FIG. 1. *Haliclona calcinea* sp. n. × 1/1.
FIG. 2. *Haliclona tenerrima* sp. n. × 3/2
Fig. 3. *Myxilla distorta* sp. n. × 1/1.
FIG. 4. *Axinella ramosa* sp. n. × 1/1.
FIG. 5. *Hymeniacidon glabrata* sp. n. × 1/1.
FIG. 6. *Halichondria cornuloides* sp. n. × 1/1.
FIG. 7. *Dragmatyle topsenti* sp. n. × 3/2.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D. A. BROWN

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ON THE POLYZOAN GENUS *CREPIDACANTHA* LEVINSEN

BY

DAVID ALEXANDER BROWN

(Geology Department, University of Otago, Dunedin, New Zealand)

Pp. 241–263 ; 4 *Text-figures*

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ON THE POLYZOAN GENUS *CREPIDACANTHA* LEVINSEN

By DAVID ALEXANDER BROWN

SYNOPSIS

The family Crepidacanthidae is considered to include only the genus *Crepidacantha* Levinsen. The known species of that genus, including two new ones, are described, and their geographic distribution discussed.

INTRODUCTION

DURING a study of the New Zealand Tertiary Cheilostomatous Polyzoa (Brown, 1952), in which the family Crepidacanthidae is moderately well represented, I have made many comparisons with material from other parts of the world. The results and conclusions concerning that family, which are beyond the scope of the Catalogue, are now put forward. Canu & Bassler (1929 : 409–412 ; 1930 : 32, 33) and Marcus (1938 : 233) have already dealt briefly with the species of *Crepidacantha*, but as their results, so far as the Indo-Pacific fauna was concerned, were probably not based on actual material, a good deal of confusion has occurred. This, I think, may now be rectified after an examination of the material in the British Museum (Natural History).

ACKNOWLEDGMENTS

My thanks are due to the Keepers of Zoology and Geology in the British Museum (Natural History) for facilities provided for my research, to the Director of Universitetets Zoologiske Museum, Copenhagen, for the loan of specimens from the Levinsen Collection, and to Dr. Anna B. Hastings and Dr. H. Dighton Thomas of the British Museum (Natural History) for their helpful criticisms of this paper.

FAMILY CREPIDACANTHIDAE

Levinsen's original definition of this family (1909 : 266) is quite adequate, though it is clear that the words " distal half " should be substituted for " proximal half " in regard to the position of the " 9–12 very long marginal spines," and that " heterozooecia " is a better term than " vibracula " in view of the large chambers occurring in *C. zelanica* Canu & Bassler which often appear to be avicularian in nature.

Genus ***Crepidacantha*** Levinsen

Crepidacantha Levinsen, 1909, Morph. Syst. Stud. Cheil. Bry. : 266 ; Brown, 1952 : 359 (*cum syn.*).

Type species (by monotypy).[1] *Crepidacantha poissonii* (Audouin) var. *crinispina* Levinsen, 1909 : 266, 267, text-figs. 1, 2, 3, 5, 6. Recent : Thailand.

The orifice of this genus has a wide poster, and the recumbent[2] ovicell has an ectooecium with an uncalcified frontal area of variable size in which the entooecium, which usually has pores, is visible. Marginal spines occur along the distal-lateral edges of the zooecia alternating with the pore-chambers which are often marked by slit-like areolae. Paired heterozooecia[3], usually vibracular in nature, with long setiform flagella, are present, either placed as tubular chambers on each side of the orifice or as rounded chambers on the frontal wall proximally to the orifice.

Bassler (1935 : 81) records the genus as ranging from Cretaceous to Recent, but I have not been able to find any records of species earlier than the Waiauan [Middle Miocene] stage of New Zealand. However, as it is even then a clearly distinct genus, it will probably be found in beds of earlier age. From the evidence available, it appears to be mainly a tropical and sub-tropical encrusting genus ranging from 0–250 fathoms, though specimens have been found in New Zealand waters as far south as Kaka Point (169° 50′ E., 46° 25′ S.).

The orifice of *Crepidacantha* is evidently similar in construction to that of the family Hippoporinidae though rather peculiar in the breadth of the shallow poster. The latter may vary considerably in shape, with a convex proximal lip as in *C. solea* Canu & Bassler (Fig. 1H) or a very concave one as in *C. setigera* Smitt sp. (Fig. 1E). However, a separate family appears to be justified in view of the nature of the orifice and of the constant occurrence of paired, symmetrically placed heterozooecia.

Canu & Bassler (1929 : 408) apparently considered the presence of a recumbent ovicell as a family character for they grouped the genera *Mastigophora* Hincks and *Schizobathysella* Canu & Bassler with *Crepidacantha* on this account (see also Canu & Bassler, 1927 : 21, where *Pachykraspedon* Koschinsky, *Nimba* Jullien and *Nimbella* Jullien are also included in the Crepidacanthidae ; and Canu & Lecointre, 1930 : 110). An examination of these genera, however, shows clearly (from the nature of the orifice, which is, in my opinion, of far greater importance from the point of view of classification than the presence of a recumbent ovicell) that they can be grouped neither with *Crepidacantha* nor together. *Mastigophora* Hincks (= *Escharina* Milne-Edwards) and *Schizobathysella* Canu & Bassler belong to the Schizoporellidae. *Nimba* Jullien and *Nimbella* Jullien appear to be closely related, and, though Jullien & Calvet (1903) placed the former in the Schizoporellidae and the latter in the Sertellidae (Reteporidae), they should probably be placed together in a separate family. *Pachykraspedon* Koschinsky probably belongs also to the Schizoporellidae as its primary orifice possesses a deep, often sub-circular sinus flanked by a pair of stout condyles; there is a thick raised peristome and a coarsely perforate frontal wall. I therefore regard the Crepidacanthidae as including only one genus, as did Levinsen.

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[1] It may be argued that Levinsen also included the species *C. poissonii* itself as a genosyntype. If this be accepted, then the selection of type must be *Flustra poissonii* Audouin, 1826, p. 240, pl. 10, figs. 5^1, 5^2, by Edwards (1910 : 21).

[2] This term appears to have been used first by Canu & Bassler (1917 : 66) and later amplified in their 1920 monograph (pp. 54, 55, text-fig. 10, " Independent (recumbent) aneucleithrian hyperstomial ovicell "). The peculiarity of this type of ovicell may be seen at the edge of a colony. Here, the ovicell is observed to be attached to the distal wall of the fertile zooecium and is fully formed before any trace of distal zooecia appears. The latter then grow round the ovicell so that it appears more or less embedded in them. In the case of the ordinary hyperstomial ovicell, the frontal wall of the distal zooecium is in process of growth at the same time as the ovicell of the proximal zooecium, the rudiment of the ovicell making its appearance on the proximal part of the frontal wall of the developing distal zooecium (see Levinsen, 1909, pl. 19, fig. 4*a*).

[3] The ancestrula on a specimen of *C. altirostris* Canu & Bassler (= *C. crinispina* Levinsen sp.) appeared to possess a single vibracular chamber (see under *C. crinispina*).

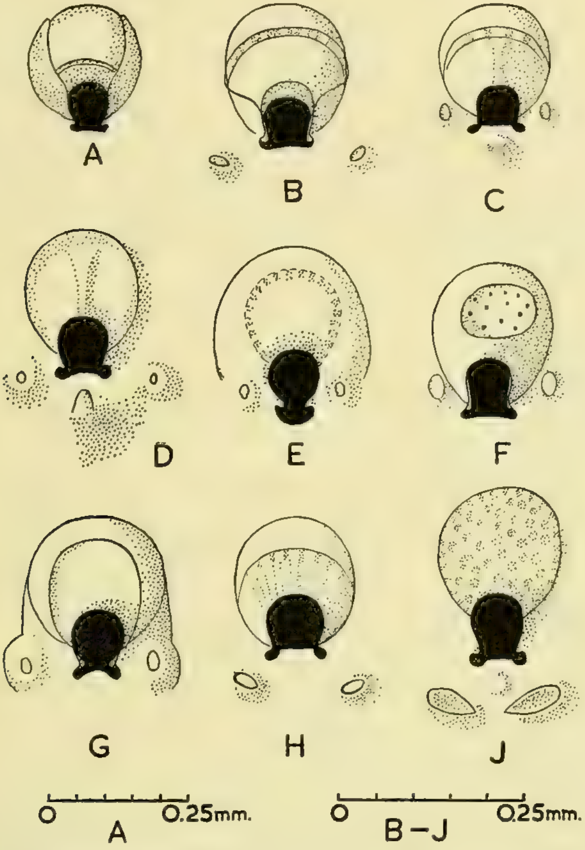

FIG. 1. Species of *Crepidacantha* showing orifice, ovicell and position of heterozooecia. A. *Crepidacantha poissonii* (Audouin) var. *teres* Hincks. Oblique view showing structure of ectooecium. B.M., 11.10.1.783. Recent: Madeira. B. The same, frontal view. C. *C. crinispina* (Levinsen). Lectotype. Recent: Bangkok, Thailand. D. *C. crinispina* (Levinsen) var. *parvipora* (Canu & Bassler). B.M., D.36894. Waiauan [Middle Miocene]: Weka Pass, New Zealand. E. *C. setigera* (Smitt). B.M., 32.3.7.27. Recent: Straits of Florida. F. *C. longiseta* Canu & Bassler. B.M., 99.7.1.1722. Recent: John Adams Bank, Brazil. G. *C. grandis* Canu & Bassler. B.M., 31.12.30.158. Recent: Philippines. H. *C. solea* Canu & Bassler. Lectotype, B.M., 89.8.21.19. Recent: Tizard Reef, China Sea. J. *C. zelanica* Canu & Bassler. B.M., D.36897. Nukumaruan [Middle Pliocene]: Petane, New Zealand.

Vigneaux's contention (1949 : 19) that the family Crepidacanthidae is superfluous and that *Crepidacantha*, along with a number of other genera, should be placed in the family Phylactellidae[1] appears to be quite without foundation. In so far as *Crepidacantha* is concerned, the only point of resemblance to *Phylactella* Hincks, 1879 [genolectotype (chosen by Canu & Bassler, 1917 : 67) : *Lepralia labrosa* Busk, 1854 : 65, 82, pl. 92, figs 1, 2, ? 3] is the possession of a recumbent ovicell.

Livingstone (1929 : 94) has stated that the position of the vibracula is of little importance in classifying the species of *Crepidacantha*. However, the orientation of the flagella (i.e., laterally or proximally) does appear to be constant within a species, and it has been found, with one exception, viz., *C. crinispina* (Levinsen) var. *parvipora* Canu & Bassler var., that where the vibracular chambers are placed proximally to the orifice, the flagella are directed laterally inwards, whereas those species with vibracular chambers alongside the orifice have their flagella directed proximally. It is found also that these differences in the orientation of the flagella are accompanied by other important distinguishing characters such as the structure of the ovicell and the shape of the zooecial orifice.

KEY TO THE SPECIES OF *Crepidacantha* DESCRIBED HERE

1. Ovicell with uncalcified area of ectooecium occupying most of the frontal area . 2.
Ovicell with uncalcified area of ectooecium much less extensive . . . . . 10.
2. Heterozooecia placed alongside orifice. Flagella directed proximally . . . 3.
Heterozooecia placed proximally to orifice. Flagella usually directed laterally inwards. 5.
3. Ovicell large. Poster very deep, concave . . . . E. *C. setigera* (Smitt).
Ovicell not large. Poster shallow, convex . . . . 4.
4. Proximal lip of orifice square and plate-like. Calcified ectooecium marginal
C. *C. crinispina* (Levinsen).
Proximal lip of orifice rounded, convex. Calcified ectooecium wide
G. *C. grandis* Canu & Bassler.
5. Heterozooecia large. Ovicell coarsely perforate . . J. *C. zelanica* Canu & Bassler.
Heterozooecia small . . . . 6.
6. Median frontal umbo much enlarged. Flagella directed proximally
D. *C. crinispina* (Levinsen) var. *parvipora* (Canu & Bassler).
Median tubercle small or absent. Flagella directed inwards . . . . . . 7.
7. Entooecium with longitudinal radiating ridges . . . . 8.
Entooecium without radiating ridges, but may have median carina . . . 9.
8. Proximal lip of orifice convex, rounded . . . A. *C. poissonii* (Audouin).
Proximal lip of orifice convex, square, plate-like . . H. *C. solea* Canu & Bassler.
9. Ovicell deeply immersed. Calcified ectooecium marginal. Proximal lip of orifice convex, square, plate-like . . . . L. *C. kirkpatricki*, sp. nov.
Ovicell globular. Calcified ectooecium covering proximo-lateral portions of ovicell. Proximal lip of orifice nearly straight . . . B. *C. poissonii* (Audouin) var. *teres* Hincks.
10. Entooecium exposed in depressed transverse oval area . F. *C. longiseta* Canu & Bassler.
Entooecium exposed in raised longitudinal oval area . K. *C. bracebridgei*, sp. nov.

A. *Crepidacantha poissonii* (Audouin)

Flustra poissonii Audouin, 1826, Description de l'Égypte : 240 ; Savigny, 1826, pl. 10, figs. 5^1, 5^2 ; Audouin, 1828 : 68.

Reptescharellina poissonii d'Orbigny, 1852, Paléontologie Française. Terr. Crét. **5** : 454.

Crepidacantha poissoni, Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 409, text-fig. 160A.

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[1] See also Canu & Bassler, 1923 : v.

DIAGNOSIS (from Savigny's figure). *Crepidacantha* with entooecium ornamented frontally with longitudinal radiating bars. Vibracula placed proximally to orifice. Proximal lip of orifice convex, rounded.

REMARKS. Audouin (1826 : 240 ; 1828 : 68) in his notes on the species figured in Savigny's plate 10, gives no locality for these, and they may, therefore, be either from the Red Sea or the Egyptian coast of the Mediterranean[1]. I have not seen any specimens from either of these localities[2] and I am unable to decide whether this species is the same as the variety from Madeira (see below). Savigny has, however, clearly figured radiating longitudinal ridges on the frontal surface of the entooecium and these do not appear on any of the specimens examined from Madeira. The proximal lip of the orifice of Audouin's species is also much more convex than that of the Madeiran material, which I have recognized, therefore, as a distinct variety, *teres* Hincks. It is unfortunate that Savigny did not indicate in his figure the orientation of the vibracular setae, but it is most probable that, as the vibracular chambers are placed proximally to the orifice, the flagella were directed laterally inwards.

DISTRIBUTION[1]. ? Eastern Mediterranean ; ? Red Sea.

B. ***Crepidacantha poissonii*** (Audouin) var. ***teres*** Hincks

(Fig. 1A, B)

Lepralia kirchenpaueri Heller var. *teres* Hincks, 1880, Ann. Mag. nat. Hist. (5) **6** : 77, pl. 9, figs. 7, 7*a* ; Hincks, 1891 : 88, 89.

Lepralia teres Hincks, 1895, Index Mar. Polyzoa : ii, note.

Lepralia poissonii Audouin, Waters, 1899, J.R. micr. Soc. : **16** ; Norman, 1909 : 307, pl. 41, figs. 7, 8 ; *L. poissoni*, Calvet, 1907 : 409.

Crepidacantha poissoni, Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 409, text-figs. 160B, C ; *C. poissonii*, Osburn, 1940 : 451 ; ? *Crepidacantha poissonii*, Canu & Bassler, 1928*a* : 136, pl. 34, fig.3.

MATERIAL EXAMINED :—

B.M., 11.10.1.783[3] (Figs. 1A, B). Recent : Madeira. Specimen encrusting small *Pecten*. Labelled "*Lepralia Poissonii* Aud. Madeira, 1897. A.M.N." Norman Collection.

B.M., 11.10.1.784. Recent : Madeira. Labelled "*Lepralia Poissonii* Audouin. Salvages. Senor D. Noronha." Norman Collection.

B.M., 11.10.1.785. Recent : Madeira. Labelled "*Lepralia Poissonii* Aud. Porto Santo. Senor de Noronha. 1908." Norman Collection.

DIAGNOSIS. *Crepidacantha* with the calcified ectooecium confined to the lateral margins of the ovicell, the entooecium with a transverse porous ridge. Vibracular flagella directed laterally. Proximal lip of orifice straight or slightly convex. Marginal spines slender, about twelve in number.

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[1] D'Orbigny (1852 : 454) cites the Red Sea for *C. poissonii*. See also Postscript.

[2] Monsieur E. Buge of the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, states (*in litt.*) that the Savigny & Audouin Collection is considered lost.

[3] Specimens in the British Museum (Natural History) are referred to by their Register Numbers.

REMARKS. The chief differences between this variety and Audouin's species have been noted above. Another important character is the proximo-lateral extension of the calcified ectooecium which covers the entooecium near the orifice. The ridge with the row of pores traversing the frontal wall of the ovicell does not mark the edge of the calcareous ectooecium, as I thought at first (Brown, 1952 : 361), but is an ornamentation of the entooecium.

DISTRIBUTION. *Recent :* Madeira ; Cape Verde Islands, 110–180 metres (Calvet) ; Porto Rico, 6 fathoms (Osburn) ; Bermuda (Osburn).

Fossil : ? Pliocene : Bocas Island, NW. Panama (Canu & Bassler).

C. *Crepidacantha crinispina* (Levinsen)

(Fig. 1C)

Lepralia poissonii Audouin, Waters, 1887, Q. J. geol. Soc. Lond. **43** : 42, 59 (part.—non pl. 8, fig. 37 = *C. zelanica* Canu & Bassler) ; Philipps, 1899 : 440, 446 ; ? *Lepralia poissonii*, Hincks, 1881 : 122 ; ? *Lepralia poissonii* (second form), Hincks, 1885 : 256.

Lepralia setigera Smitt, MacGillivray, 1883, Trans. roy. Soc. Vict. **19** : 133, pl. 1, figs. 2, 3 ; MacGillivray, 1887 : 212.

? *Crepidacantha poissoni* Livingstone, 1929, Vidensk. Medd. dansk naturh. Foren. Kbh. **87** : 93.

Crepidacantha poissonii Audouin var. *crinispina* Levinsen, 1909, Morph. Syst. Stud. Cheil. Bry. : 266, text-figs. 1, 2, 3, 5, 6 ; *C. poissoni* var. *crinispina*, Canu & Bassler, 1923 : 174, text-figs. 33A–C, E, F.

Crepidacantha setifera Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 409 ; Canu & Bassler, 1930 : 32, 33.

Crepidacantha papulifera Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 410, text-figs. 160K, 161B, pl. 57, fig. 8.

Crepidacantha crinispina (Levinsen), Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 409, text-figs. 160D–F, H, I ; Brown, 1952 : 359, text-fig. 283 ; Brown, 1954 : 433.

Crepidacantha altirostris Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 411, pl. 57, fig. 9.

LECTOTYPE (chosen by Brown, 1952 : 359). Universitetets Zoologiske Museum, Copenhagen, specimen encrusting fragment of large lamellibranch (Fig. 1C). Recent : Koh Kram, Bangkok, Thailand, 30 fathoms. Levinsen Collection.

OTHER MATERIAL EXAMINED :—

B.M., 97.5.1.832, 835. Recent : Port Phillip Heads, Victoria. Two encrusting specimens. Labelled "*Lepralia setigera.*" Bracebridge Wilson Collection.

B.M., 88.11.14.307. Recent : Port Phillip, Victoria. Labelled "*Lepralia poissonii* Aud." by Kirkpatrick. Bracebridge Wilson Collection.

B.M., 99.5.1.825. Recent : Wellington, New Zealand. Labelled "*Lepralia Poissonii* Audouin" by Miss Jelly. Hincks Collection.

B.M., 31.12.30.157. Recent : *Albatross* Stn. 5179, 37 fathoms off Romblon Light, Romblon, Philippines. Paratype of *C. altirostris* Canu & Bassler. Presented by the U.S. National Museum.

B.M., D.36893. Castlecliffian CU3 [Upper Pliocene] : Castlecliff, New Zealand. Sent by Mr. C. A. Fleming.

Waitotaran [Middle Pliocene] : submarine limestone off Three Kings Islands, New Zealand.

DIAGNOSIS. *Crepidacantha* with the calcified ectooecium confined to the distal-lateral margins of the ovicell. Entooecium with a longitudinal median carina. Vibracula placed alongside the opercular condyles, the flagella directed proximally. Proximal lip of orifice convex, often plate-like. Frontal wall of zooecium often bearing a prominent sub-oral tubercle. Marginal spines ten in number.

REMARKS. In addition to the comments already made on this species by Brown (1952 : 360) the following remarks are apposite.

This species is clearly distinct from both *C. poissonii* (Audouin) and from *C. poissonii* var. *teres* in the different construction of its ovicell and in the position and orientation of its vibracular setae.

In the lectotype the ovicells have marked eversion of the transverse ridge, which tends to be masked in the Australian and New Zealand specimens by thickening of the ectooecium.

Although MacGillivray (1883 : 133, pl. 1, fig. 2) does not show the median carina on the ovicell of his *Lepralia setigera* Smitt, there can be little doubt that this is the species described by him, as it differs completely from the other species of *Crepidacantha* from Port Phillip, Victoria, namely, *C. bracebridgei*, sp. n., and *C. kirkpatricki*, sp. n. This identification is substantiated by two specimens from Port Phillip Heads sent by Mr. J. Bracebridge Wilson and labelled by him "*Lepralia setigera*" (B.M., 97.5.1.832, 835). Canu & Bassler's name, *C. setifera* (1929 : 409), proposed for *Lepralia setigera* MacGillivray, must therefore lapse in favour of Levinsen's name, *C. crinispina*.

The specimen (B.M., 88.11.14.307) from Port Phillip, Victoria, has a very marked sub-oral umbo resembling that of *C. crinispina* (Levinsen) var. *parvipora* Canu & Bassler var. from New Zealand, but the plate-like proximal lip of the orifice and the rather distally placed vibracula distinguish it from that variety.

In the Recent specimen (B.M., 99.5.1.825) from Wellington, New Zealand, the vibracular chambers are rather larger than those of the lectotype and the sub-oral tubercle is often absent : it is probably *C. crinispina*.

Canu & Bassler's reasons for separating *C. papulifera* (1929 : 409, text-fig. 160K ; 410, 411, text-fig. 161B, pl. 57, fig. 8) from *C. crinispina* appear to be without foundation.

C. altirostris Canu & Bassler (1929 : 411, pl. 57, fig. 9) is represented in the British Museum (Natural History) by a paratype (B.M., 31.12.30.157) and appears to be conspecific with *C. crinispina*. The vibracula are sometimes placed near the distal end of the zooecium as stated by Canu & Bassler, but this feature is also seen in the lectotype of Levinsen's species. The only difference to be seen in the specimen of *C. altirostris* is the rather more marked carination of the entooecium which shows no eversion of the transverse ridge. The ancestrula is preserved in this specimen. It is small and appears to have a single vibraculum placed proximally and to one side of the orifice.

DISTRIBUTION. *Recent :* Thailand (30 fathoms) ; Philippines (21–105 fathoms) ; Port Phillip, Victoria ; Loyalty Islands, New Caledonia (35 fathoms) (Philipps) ; ? Bass Strait (Hincks) ; New Zealand (3–10 fathoms).

Fossil : Castlecliffian [Upper Pliocene] : Castlecliff ; ? Shakespeare Cliff, New

Zealand. ? Nukumaruan [Middle Pliocene] : Waipukurau, New Zealand (Waters). Waitotaran [Middle Pliocene] : submarine limestone off Three Kings Islands, New Zealand.

D. *Crepidacantha crinispina* (Levinsen) var. *parvipora* (Canu & Bassler)

(Fig. 1D)

Lepralia poissonii Audouin (third form), Hincks, 1885, Ann. Mag. nat. Hist. (5) **15** : 256 ; *L. poissonii*, Waters, 1887 : 59 (part.—non pl. 8, fig. 37 = *C. zelanica* Canu & Bassler).
Crepidacantha parvipora Canu & Bassler, 1930, Proc. U.S. nat. Mus. **76** (13) : 32, 33.
Crepidacantha crinispina (Levinsen) var. *parvipora*, Brown, 1952, Tert. Cheil. Polyzoa N. Zealand : 361, text-fig. 284.

NEOTYPE (chosen by Brown, 1952 : 361). B.M., D.37042. [Pliocene] : [Napier], New Zealand. Labelled " *Lepralia Poissonii* var. R. Tert. N. Zealand " by Miss Jelly. Hincks Collection.

OTHER MATERIAL EXAMINED :—

B.M., D.36777. Nukumaruan [Middle Pliocene] : Waipukurau Gorge. Encrusting specimen. Hincks Collection.

B.M., D.32531. Nukumaruan [Middle Pliocene] : Waipukurau Gorge. Encrusting specimen. Labelled "*Lepralia Poissonii* Aud." by Miss Jelly. Hincks Collection.

B.M., D.36894 (Fig. 1D)–36896. Waiauan [Middle Miocene], Base of Uppermost Mt. Brown " E " Limestone : Junction of Weka Creek and Weka Pass Stream, Waipara, S.D. Three encrusting specimens. Sent by Professor B. H. Mason.

DIAGNOSIS. *C. crinispina* with a stout median ridge on the frontal wall ending distally in a sub-oral umbo. Vibracula placed on either side of the umbo, the flagella directed proximally.

REMARKS. This variety has been fully discussed by Brown (1952 : 361). Unlike the other known species of *Crepidacantha* in which the vibracula are placed proximally to the orifice, this variety has the flagella directed proximally. The presence of the marked sub-oral umbo would inhibit or prevent the inward turning of the vibracula.

DISTRIBUTION. *Fossil :* Nukumaruan [Middle Pliocene] : [Napier] ; Waipukurau Gorge, New Zealand. Waiauan [Middle Miocene] : Weka Pass, New Zealand.

E. *Crepidacantha setigera* (Smitt)

(Fig. 1E)

Escharella setigera Smitt, 1873, K. svensk. Vetensk.—Akad. Handl. **11** (4) : 58, 75, 82, pl. 10, fig. 206.
Crepidacantha setigera, Canu & Bassler, 1928*a*, Proc. U.S. nat. Mus. **72** (14) : 135, pl. 21, fig. 10 ; Canu & Bassler, 1929 : 409 ; Osburn, 1940 : 452 ; Osburn, 1952 : 479, pl. 58, fig. 1.

MATERIAL EXAMINED :—

B.M., 32.3.7.27 (Fig. 1E). Recent : *Albatross* Stn. 2639, Straits of Florida. Two encrusting specimens. Presented by the U.S. National Museum.

DIAGNOSIS. *Crepidacantha* with large ovicell not clearly separated from the zooecium, the entooecium with a curved row of pores, the ectooecium wide.

Vibracula placed just above the level of the opercular condyles, the flagella directed proximally. Poster very deep and concave.

REMARKS. This species is very clearly distinguished by the shape of its orifice and its large ovicell. Smitt (1873 : 57, 82) regarded it as a variety of *Lepralia depressa* Busk (1854 : 75, pl. 91, figs. 3, 4), to which, however, it does not seem to be related.

Osburn's record (1952: 479) of this species from the Galapagos Islands is interesting. Whether the distribution of this and other Polyzoan species, now living on both sides of the Isthmus of Panama, indicates a geologically recent connection or is due to transport of larvae and colonies on, for instance, the bottoms of ships traversing the canal, will probably never be known. It is likely, however, that the fresh-water Gatun Lake would be an efficient barrier to such a passage.

DISTRIBUTION. *Recent :* Gulf of Mexico (50–60 fathoms) : Galapagos Islands (Osburn).

F. *Crepidacantha longiseta* Canu & Bassler

(Fig. 1F)

Lepralia poissonii Audouin, Kirkpatrick, 1888*a*, Ann. Mag. nat. Hist. (6) **1** : 78, pl. 8, fig. 1 ; ? *L. poissonii*, Thornely, 1912 : 150 ; Waters, 1914 : 856.

Crepidacantha longiseta Canu & Bassler, 1928*a*, Proc. U.S. nat. Mus. **72** (14) : 135, pl. 21, figs. 3, 4 ; Osburn, 1940 : 452.

Crepidacantha levinseni Marcus, 1938, Vidensk. Medd. dansk naturh. Foren. Kbh. **101** : 231 (part.), text-figs. 28A, B.

HOLOTYPE. U.S. National Museum No. 7826. Recent : Cuba.

MATERIAL EXAMINED :—

B.M., 88.1.25.31. Recent : Mauritius. Labelled "*Lepralia Poissonii* Audouin." V. Robillard Collection.

B.M., 34.10.6.19. Recent : Mauritius.

B.M., 99.7.1.1722 (Fig. 1F). Recent : John Adams Bank, South Atlantic, off Brazil. Labelled " *Lepralia Poissonii* Aud." Busk Collection.

DIAGNOSIS. *Crepidacantha* with porous entooecium visible through a transverse, sub-circular or oval fenestra in the ectooecium. Vibracular chambers tubular, placed at the level of the opercular condyles, the flagella very long and directed proximally. Proximal lip of orifice straight or slightly concave. Marginal spines ten in number.

REMARKS. I have not examined any West Indian material of *C. longiseta*, but a specimen (B.M., 99.7.1.1722, Busk Coll., collected by H.M.S. " Herald " from the John Adams Bank off the coast of Brazil), undoubtedly represents that species. This specimen also agrees closely with the *lectotype* (*here chosen*) of Marcus's *C. levinseni* from St. Helena (viz., the specimen figured by him, 1938, text-fig. 28A on p. 232), except that the porous area (entooecium) in the ectooecium of the Brazilian specimen appears to be quite separated from the orifice (Fig. 1F). As shown later, the species from Port Phillip, Victoria, with which Marcus correlated his *C. levinseni*, is new, namely, *C. kirkpatricki*.

The original material from Mauritius described by Kirkpatrick as *Lepralia Poissonii* Audouin (B.M., 88.1.25.31), and another specimen from the same locality (B.M., 34.10.6.19) are conspecific. They differ from the Brazilian material only in having a slightly longer orifice and in having a rather coarsely granular frontal wall.

Marcus (1938 : 233–234 key and distribution statements) working, as he explained, from the literature without material for examination, described the ovicell area of *C. longiseta* as without pores, thus distinguishing it from *C. levinseni.* He did, however, refer the Mauritius form to *C. longiseta,* but also regarded the form from the China Sea (*C. solea*) as synonymous.

Osburn (1940 : 452 ; 1952 : 479) thought that *C. longiseta* might be synonymous with *C. setigera* (Smitt), but the ovicell and the orifice of the latter species are clearly distinctive.

DISTRIBUTION. *Recent :* Cuba (67–201 fathoms) (Canu & Bassler) ; John Adams Bank, Brazil ; St. Helena (36–69 metres) (Marcus) ; Mauritius ; ? Zanzibar (Waters) ; ? Providence, NNE. Madagascar (50–78 fathoms) (Thornely).

G. ***Crepidacantha grandis*** Canu & Bassler

(Fig. 1G)

Crepidacantha grandis Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 411, text-figs. 160L, 161A, pl. 57, figs. 4–7.

SYNTYPES. U.S. National Museum No. 8220. Recent : Philippines.

MATERIAL EXAMINED :—

B.M., 31.12.30.158 (Fig. 1G). Recent : *Albatross* Stn. 5217, 105 fathoms, Ragay Gulf, off North Burias, Philippines, in coarse, grey sand.

DIAGNOSIS. *Crepidacantha* with large zooecia, the calcified ectooecium confined almost entirely to the distal-lateral edges of the ovicell. Vibracula placed at the level of the large opercular condyles, the flagella directed proximally. Proximal lip of orifice very convex and rounded.

REMARKS. This species appears to be quite distinct. Canu & Bassler state (1929 : 412) that on the " nonmarginal zooecia the setiform spines [spines arising from the marginal portions of the zooecia] are short (= 0·15 – 0·20 mm.) and all equal ; they are very long on the contrary (= 0·60 mm.) on the free side of the marginal zooecia."

In a number of zooecia in the British Museum specimen (B.M., 31.12.30.158) the frontal wall is punctured by a large rounded hole through which, presumably, the polypide was extracted for food by some predatory borer.

DISTRIBUTION. *Recent :* Philippines (105 fathoms).

H. ***Crepidacantha solea*** Canu & Bassler

(Fig. 1H)

Lepralia poissonii Audouin (first form), Hincks, 1885, Ann. Mag. nat. Hist. (5) **15** : 256 (part.) ; *L. poissonii,* Kirkpatrick, 1890 : 16.

Crepidacantha poissonii, Canu & Bassler, 1928*b*, Bull. Soc. Sci. nat. méd. Seine-et-Oise (2) **8** (7) suppl. : 37, pl. 8, fig. 7 ; Canu & Bassler, 1930 : 33, pl. 5, fig. 5 ; *C. poissoni*, Osburn, 1952 : 478, pl. 58, fig. 2.

Crepidacantha solea Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 409 ; Canu & Bassler, 1930 : 32.

LECTOTYPE (here chosen). B.M., 89.8.21.19 (Fig. 1H). Recent : Tizard Reef, China Sea, 27 fathoms. Specimen encrusting lamellibranch. Labelled " *Lepralia poissonii* Aud." by Kirkpatrick. H.M.S. " Rambler " Collection.

OTHER MATERIAL EXAMINED :—

B.M., 97.5.1.828. Recent : Tahiti. Labelled "*Lepralia Poissonii* Aud." by Miss Jelly. Bracebridge Wilson Collection.

B.M., 99.5.1.824. Recent : Tahiti. Labelled " *Lepralia Poissonii* Aud. 791. Avicularia horizontal " by Miss Jelly. Hincks Collection.

Note. Another slide, B.M., 99.5.1.823, Hincks Collection, similarly labelled, has no specimen.

DIAGNOSIS. *Crepidacantha* with a prominent transverse ridge across the entooecium which also has a faint median carina and traces of longitudinal markings. Calcified ectooecium confined to the distal-lateral margins. Vibracula large, placed proximally to the orifice, the flagella directed laterally inwards. Proximal lip of orifice square, plate-like.

REMARKS. Canu & Bassler (1929 : 409) introduced the name *Crepidacantha solea* for " *Lepralia poissonni* [*sic*], Kirkpatrick, 1888, from Mauritius, Sea of China and Australia." Kirkpatrick's material from these localities is preserved in the British Museum collections and proves to belong to three different species. Later (1930 : 32), however, Canu & Bassler restricted the name *C. solea* to Kirkpatrick's material from the China Sea (1890 : 16) and the species is here understood in that sense.

C. solea is, indeed, very closely related to the original *Flustra poissonii* Audouin, especially in the appearance of faint longitudinal markings[1] on the frontal part of the entooecium. It is distinguished by its large vibracula placed more proximally than usual and by the square plate-like lip of the orifice.

Hincks (1885 : 256) recorded two forms of "*Lepralia Poissonii*, Audouin " from Tahiti. The first, in which " . . . the vibracula are situated below the orifice and are placed horizontally," is undoubtedly the present species as shown by Hincks's material (B.M., 97.5.1.828 and B.M., 99.5.1.824). The second (B.M., 99.5.1.825), with vertical vibracula placed alongside the orifice, is probably *C. crinispina* (Levinsen).

It is evident that the material from the Hawaiian Islands and the Galapagos Islands, identified by Canu & Bassler (1928*b* : 37 ; 1930 : 32, 33) as *C. poissonii*, can also be placed here, as well as Osburn's material from the American Pacific coast (1952 : 478, pl. 58, fig. 2).

DISTRIBUTION. *Recent :* Tizard Bank, China Sea (27 fathoms) ; Tahiti ; Hawaii (130–250 fathoms) (Canu & Bassler) ; Galapagos Islands (33–40 fathoms) (Canu & Bassler) ; American Pacific coast (Osburn).

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[1] See Postscript.

J. ***Crepidacantha zelanica*** Canu & Bassler

(Fig. 1J)

Lepralia poissonii Audouin (first form), Hincks, 1885, Ann. Mag. nat. Hist. (5) **15** : 256 (part.) ; *L. poissonii*, Waters, 1887 : 59 (part.), pl. 8, fig. 37.

Crepidacantha poissoni (?) Waters, Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 409, text-fig. 160J.

Crepidacantha zelanica Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 410 ; Canu & Bassler, 1930 : 32, 33 ; Brown, 1952 : 362, text-figs. 285, 286.

NEOTYPE (chosen by Brown, 1952 : 362). B.M., 99.5.1.826. Recent: Napier, New Zealand. Specimen encrusting pebble. Labelled " *Lepralia Poissonii*, Aud." by Miss Jelly. Hincks Collection.

OTHER MATERIAL EXAMINED :—

Recent : Waitarere Beach, Wellington, 25 fathoms. Specimen encrusting concretion. Geology Department, Otago University.

Recent : Kaka Point, Southland, New Zealand. Specimen encrusting *Atrina zelandica* (Gray). Geology Department, Otago University.

B.M., D.32531. Nukumaruan [Middle Pliocene] : Waipukurau Gorge. Encrusting specimen. Labelled "*Lepralia Poissonii* Aud." by Miss Jelly. Hincks Collection.

B.M., D.36901. Nukumaruan [Middle Pliocene] : Napier Harbour. Encrusting specimen. Hincks Collection.

B.M., D.1430, D.1431. Nukumaruan [Middle Pliocene] : Petane. Two encrusting specimens. Labelled "*Lepralia Poissonii* Aud." by Miss Jelly. Vine Collection.

B.M., D.36897 (Fig. 1J)–36900. Nukumaruan [Middle Pliocene] : Petane. Four encrusting specimens. Blake Collection.

Nukumaruan [Middle Pliocene] : Waipukurau. Encrusting specimen. Labelled "*Lepralia Poissonii*" by Waters. Waters Collection, Manchester Museum.

Nukumaruan [Middle Pliocene] : Petane. Encrusting specimen. Labelled "*Lepralia Poissonii*" by Waters. Waters Collection, Manchester Museum.

DIAGNOSIS. *Crepidacantha* with uncalcified area of ectooecium occupying most of the frontal surface of the globular ovicell, exposing coarsely perforate entooecium. Heterozooecia large, prominent, placed proximally to the orifice, the flagella directed inwards. Orifice with slightly convex proximal lip.

REMARKS. This species has been fully discussed by Brown (1952 : 362). In the Recent specimen from Kaka Point, Southland, the heterozooecia, although fairly large in size, are still vibracular in nature and have pronounced setiform flagella.

The first form of "*Lepralia Poissonii*, Audouin" recorded from New Zealand by Hincks (1885 : 256) is almost certainly this species though no material labelled by Hincks is available.

DISTRIBUTION. *Recent :* Napier ; Wellington ; Kaka Point, New Zealand.

Fossil : Nukumaruan [Middle Pliocene] : Petane ; Waipukurau Gorge ; Napier Harbour.

K. ***Crepidacantha bracebridgei***[1] sp. nov.

(Fig. 2)

HOLOTYPE. B.M., 88.11.14.224 (Fig. 2). Recent: Port Phillip Heads, Victoria. Specimen encrusting lamellibranch shell. Slide labelled "*Lepralia poissonii* Audn." by Kirkpatrick. Bracebridge Wilson Collection.

OTHER MATERIAL EXAMINED :—

B.M., 88.11.14.434. Paratype. Recent: Port Phillip Heads. Encrusting specimen. Labelled "*Lepralia*. Jan. 1887" by Kirkpatrick. Bracebridge Wilson Collection.

B.M., 97.5.1.833. Paratype. Recent: Port Phillip Heads. Encrusting specimen. Labelled "*Lepralia setigera*. 1883" by J. Bracebridge Wilson. Bracebridge Wilson Collection.

B.M., 88.11.14.116. Paratype. Recent: Port Phillip Heads. Encrusting specimen. Labelled "*Lepralia setigera* MacG. 1884" by J. Bracebridge Wilson. Bracebridge Wilson Collection.

DIAGNOSIS. *Crepidacantha* with the porous entooecium visible in a narrow, oval, longitudinal fenestra in the ectooecium. Vibracula placed on the distal side of the opercular condyles, the flagella very long and directed proximally. A prominent sub-oral tubercle usually present. Orifice long and narrow with a convex proximal lip.

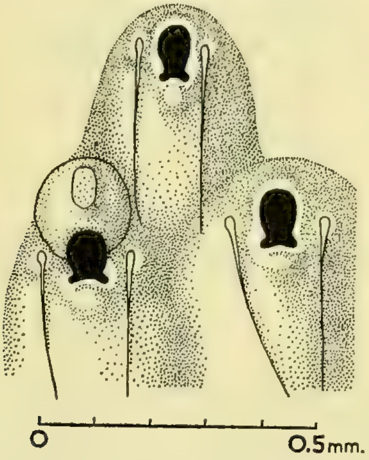

FIG. 2. *C. bracebridgei*, sp. nov. Holotype, B.M., 88.11.14.224.
Recent: Port Phillip Heads, Victoria.

DESCRIPTION. *Zoarium* encrusting.

Zooecia ovate or hexagonal, arranged quincuncially in radiating rows, distinctly separated by deep furrows. *Orifice* elongate, divided into an oval anter and a shallow poster, with a convex or squared proximal lip, the opercular condyles strong. *Peristome* thin and raised distally into a hood on non-ovicelled zooecia. *Frontal*

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[1] After Mr. J. Bracebridge Wilson, the Australian naturalist.

wall ventricose, finely granular and porous, with a prominent sub-oral tubercle. *Marginal spines* about twelve in number.

Vibracula paired, placed above the level of the opercular condyles, the flagella directed proximally and reaching beyond the proximal margins of the zooecium.

Ovicells globular, hyperstomial, longer than wide, with the uncalcified area of the ectooecium small, longitudinally-oval, placed towards the distal end of the ovicell, somewhat raised. Often a distinct umbo at its proximal end. Exposed entooecium porous.

MEASUREMENTS. $L_z = 0{\cdot}50$–$0{\cdot}55$ mm. ; $l_z = 0{\cdot}29$–$0{\cdot}33$ mm.
$h_r = 0{\cdot}08$–$0{\cdot}09$ mm. ; $l_r = 0{\cdot}07$–$0{\cdot}08$ mm.

REMARKS. The ovicell of this species is very distinctive and differs from that of *C. longiseta* in that the porous area is always raised and not depressed or surrounded by salient walls as it is in the latter species. The area is, moreover, usually placed transversely in *C. longiseta*. The presence of a sub-oral tubercle in the Australian species is probably of no great significance as its size appears to vary with the age of the zooecia, but the hooded peristome of the non-ovicelled zooecia may be an important character.

Although two of the specimens mentioned above in the Bracebridge Wilson Collection (B.M., 97.5.1.833 and B.M., 88.11.14.116) are labelled "*Lepralia setigera*," they do not belong to the species described by MacGillivray as *Lepralia setigera* Smitt (1883 : 133, pl. 1, figs. 2, 3) as his description and figure of the ovicell are clearly those of *C. crinispina* Levinsen sp.

DISTRIBUTION. *Recent :* Port Phillip Heads, Victoria.

L. ***Crepidacantha kirkpatricki***[1] sp. nov.

(Fig. 3)

Lepralia poissonii Audouin, Kirkpatrick, 1888*b*, Ann. Mag. nat. Hist. (6) **2** : 14.
Lepralia poissonii Audouin var. Waters, 1889, J. R. micr. Soc. : 14, pl. 2, fig. 17.
Crepidacantha poissonii Audouin var. Levinsen, 1909, Morph. Syst. Stud. Cheil. Bry. : 268, text-fig. 4 ; Canu & Bassler, 1923 : 174, text-fig. 33D.
Crepidacantha crinispina Levinsen var. Canu & Bassler, 1929, Bull. U.S. nat. Mus. **100** (9) : 410, text-fig. 160G.
Crepidacantha levinseni Marcus, 1938, Vidensk. Medd. dansk naturh. Foren. Kbh. **101** : 231 (part.—non text-figs. 28A, B).

HOLOTYPE. B.M., 88.11.14.426 (Fig. 3). Recent : Port Phillip Heads, Victoria. Specimen encrusting *Fucus*. Labelled "*Lepralia poissonii* Audn." by Kirkpatrick and "Jan. 1887" by J. Bracebridge Wilson. Bracebridge Wilson Collection.

OTHER MATERIAL EXAMINED :—

B.M., 97.5.1.834. Paratype. Recent : Port Phillip Heads. Labelled "*Lepralia setigera.* 1885" by J. Bracebridge Wilson. Bracebridge Wilson Collection.

Paratype : Universitetets Zoologiske Museum, Copenhagen No. 1/8/90. Recent : Port Phillip Heads. Levinsen Collection.

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[1] After the late Dr. R. Kirkpatrick, formerly of the Department of Zoology, British Museum (Natural History).

DIAGNOSIS. *Crepidacantha* with the ovicell flattened and deeply immersed in the distal zooecium, the uncalcified area of the ectooecium occupying almost the whole of the exposed frontal surface. Vibracula placed proximally to the orifice, the flagella short and directed laterally inwards. A small sub-oral tubercle present. Proximal lip of orifice squared, plate-like. Marginal spines of mature zooecia short and thick, of marginal zooecia long and flexible.[1]

DESCRIPTION. *Zoarium* encrusting.

Zooecia ovate, arranged somewhat irregularly in radiating rows, scarcely separated by shallow furrows. *Orifice* sub-circular distally with a shallow poster separated by inconspicuous condyles, the proximal lip square and plate-like. *Peristome* thin, scarcely raised. *Frontal wall* usually flattened, occasionally ventricose, finely perforate and covered with small papillae, a small, sub-oral tubercle often present. *Marginal spines* of mature zooecia short and thick, eight in number, those of the young zooecia long and flexible.

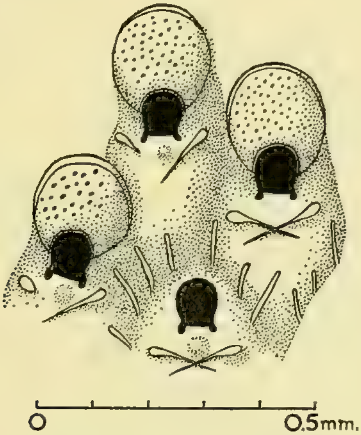

FIG. 3. *C. kirkpatricki*, sp. nov. Holotype, B.M., 88.11.14.426.
Recent: Port Phillip Heads, Victoria.

Vibracula paired, placed proximally to and on each side of the orifice, the short flagella directed obliquely laterally inwards.

Ovicells large, sub-circular in outline, deeply immersed in mature zooecia, the exposed frontal surface flattened and occupied almost entirely by a porous entooecium, the calcified ectooecium marginal.

MEASUREMENTS. $L_z = 0{\cdot}35\text{–}0{\cdot}40$ mm.; $l_z = 0{\cdot}25\text{–}0{\cdot}28$ mm.
$h_r = 0{\cdot}09\text{–}0{\cdot}10$ mm.; $l_r = 0{\cdot}07\text{–}0{\cdot}08$ mm.

REMARKS. The holotype is part of the material described by Kirkpatrick (1888*b* : 14) as *Lepralia Poissonii*, Audouin. I have also examined the specimen described by Levinsen (1909 : 268) as *Crepidacantha poissoni* var., which was kindly lent by Dr. P. L. Kramp of Universitetets Zoologiske Museum, Copenhagen, and this proves to be a small fragment, also encrusting *Fucus*, which was sent to Levinsen by Miss Jelly in 1890. It is unquestionably from the same material, if not from the same colony, as the holotype.

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[1] See Postscript for further information about this species.

This is also the species described by Waters (1889 : 14) from Green Point, New South Wales, in which the ovicells are "immersed, showing, however, a round ovicellular area on a level with the wall of the zooecium." Canu & Bassler (1929 : 410) thought that this probably belonged to another genus.

This species is closely related to *C. solea* Canu & Bassler, but differs from it in having a large, flattened ovicell and eight stout marginal spines, the spines of *C. solea* being slender and 12 to 14 in number. In *C. kirkpatricki* the surface of the zoarium is fairly even and the zooecia are not usually separated by furrows but are indistinctly merged with one another. The proximal lip of the orifice is a distinct median plate inclined to turn upwards and outwards from the orifice, the lateral indentations appearing as small sub-circular openings.

Marcus (1938 : 231), in proposing the new name *C. levinseni* for Levinsen's variety of *C. poissonii* (1909 : 268) and for his own material from St. Helena, stated that he had not seen the Port Phillip Heads material. As shown above, the St. Helena species is most probably *C. longiseta* Canu & Bassler.

DISTRIBUTION. *Recent:* Port Phillip Heads, Victoria; Green Point, Port Jackson, N.S.W. (Waters).

M. ***Crepidacantha odontostoma*** (Reuss)

Lepralia odontostoma Reuss, 1874, Denkschr. Akad. Wiss. Wien. **33** : 156, pl. 4, fig. 8.
Crepidacantha (*Lepralia*) *odontostoma*, Canu & Bassler, 1930, Proc. U.S. nat. Mus. **76** (13) : 32.

REMARKS. Without seeing Reuss's material, which comes from the Miocene of "Rauchstallbrunngraben bei Baden," it is difficult to decide on the generic affinities of this species. The orifice has a straight or slightly concave proximal lip and the paired heterozooecia are placed at the level of the opercular condyles. If this is a species of *Crepidacantha* and if the preservation is as good as Reuss's figure suggests, then one would expect to see some traces of marginal areolae. The absence of ovicells makes identification even more difficult.

DOUBTFUL REFERENCES TO SPECIES OF *Crepidacantha*

Thornely has recorded *Lepralia poissonii* Audouin from Ceylon (1905 : 119) and the Andamans[1] (1907 : 190). It is impossible to identify the species, but, from comparison with the world distribution map (Fig. 4), it is possible that *C. longiseta* Canu & Bassler or *C. crinispina* Levinsen sp. is represented here.

Waters (1914 : 832, 856) recorded *Lepralia poissonii* Audouin from the Atlantic [? = *C. poissonii* var. *teres*], Indian Ocean [? = Thornely's record, probably *C. longiseta*], Australia, and Japan. I did not see Waters's material from these localities in the collections at Manchester Museum, and, therefore, I cannot suggest to which species the Australian and Japanese records refer.

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[1] A specimen (B.M., 84.3.25.1, Wilmer Collection) from the Andaman Islands, labelled "*Lepralia poissonii* Aud." by Kirkpatrick, is not a *Crepidacantha*.

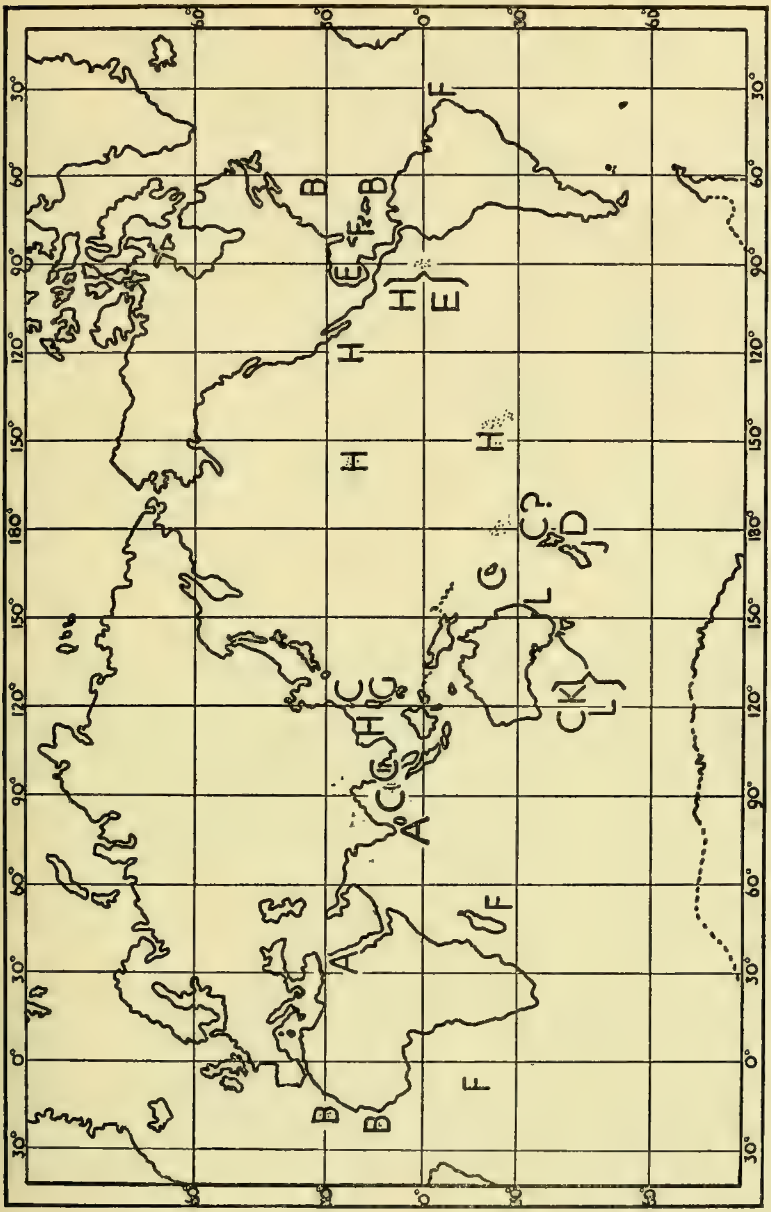
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FIG. 4. Recent distribution of species of *Crepidacantha*. Species are indicated by the index letters used throughout the text.

CONCLUSIONS

The known species of *Crepidacantha* Levinsen are 11 or 12 in number and, until recently, had been recorded only from tropical and sub-tropical waters. They have recently been found, however, as far south as Kaka Point, Southland, New Zealand (169° 50′ E., 46° 25′ S.), on a coast-line swept by a northerly drift. This is in accordance with their presence in rocks of Nukumaruan [Middle Pliocene] age in Hawkes Bay. This region (about 40° S.) has been shown by Fleming (1944) from molluscan evidence to be the northern limit of subantarctic waters in Nukumaruan times. Species of *Crepidacantha* are also plentiful in the Waiauan [Middle Miocene] rocks of North Canterbury, New Zealand, rocks deposited when New Zealand was experiencing a tropical climate.

In the northern hemisphere *Crepidacantha* has not been recorded north of Madeira (33° N.), though Waters's record from Japan (1914 : 832), if correct, may extend this range.

The first species described, *Flustra poissonii* Audouin, is not at all cosmopolitan in distribution, and, in fact, appears to be restricted to the Eastern Mediterranean or Red Sea area.[1] The accompanying map (Fig. 4) shows the known distribution of the various species.

POSTSCRIPT[2]

Dr. Anna B. Hastings, *in litt.*, writes :

" In his forthcoming, posthumous 'Siboga' Report, Sir Sidney Harmer remarks that a revision of the genus *Crepidacantha* is urgently needed.

" Pending such a revision he has recognized only two species in the Indo-Malayan, region—*C. poissonii* and *C. crinispina*—and has given tentative synonymies referring much of the previously recorded material to one or other of these species. You have now provided the necessary revision discriminating more species in this material and superseding (although ante-dating) Harmer's synonymies, which, but for the war of 1939–1945, might have been published ten years ago.

" Certain material which, as you mention, was not available when you did your work was considered by Harmer and has since been presented by him to the British Museum (Natural History). I have examined the specimens and you may like to include some notes about them :

" 1. Two specimens from Ghardaqa on the Egyptian coast of the Red Sea (Crossland, 4.P on slides 4.G^1 and 4.G^3 of *Arachnopusia spathulata*). The material 'agrees closely with Savigny's fig. 5^2 (Pl. X) except in not showing radial markings on the ovicell' (Harmer MS.).

" In the absence of any record of *Crepidacantha* from the Mediterranean, the presence on the Red Sea coast of Egypt of a species agreeing closely with Savigny's figure strongly suggests that the material of Savigny & Audouin came from the Red Sea. I am prepared to accept the two specimens from Ghardaqa as representing true *C. poissonii*.

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[1] See Postscript.

[2] The information given in this Postscript is incorporated in the distribution-map.

"*C. poissonii* (as represented by the Ghardaqa specimens) and *C. solea* are, as you have suggested, very closely related. They may perhaps be distinguished by the more proximal position of the heterozooecia in *C. solea* (which are directed laterally inwards in both species), but the Ghardaqa material shows some variation in this character. The ovicells of both show the proximo-lateral calcareous layer described by you in *C. poissonii* var. *teres*, where it is sometimes conspicuous for its opaque whiteness. They also agree with that variety in having a porous, transverse ridge on the ovicell. The pores are, however, more or less obscured by a membranous layer (membranous part of the ectooecium). The appearance depends very much on the direction of the light. Illuminated from the proximal end the membrane covering the frontal surface shines and, being stretched in drying, may give an impression of some radial striation, and the pores are hidden. Illuminated from the distal end the membranous layer is inconspicuous and the transverse row of pores may be observed. Such effects as this probably account for the absence of any appearance of the row of pores on the entooecium in your figures of *C. crinispina* var. *parvipora* both here (Fig. 1D) and in the Catalogue (Brown, 1952 : 361, text-fig. 284) and of typical *C. crinispina* (Catalogue, text-fig. 283).

" 2. Thornely's Ceylon specimen (Thornely Coll., 1906, no. 46). This specimen agrees very closely with the Ghardaqa specimens of *C. poissonii*. It has one ovicell, which shows the membrane, the row of pores, and the proximo-lateral calcareous ectooecium as described above.

" 3. Thornely's Andaman specimen (Thornely Coll., 1935, no. 118). This belongs to *C. crinispina* as limited by you.

" 4. A specimen from Victoria (Cambridge Museum, E. C. Jelly, May 24, 1895) is also of interest. Harmer (MS.) mentions it as probably representing a new species. It has no ovicells, but in other respects agrees with the type-specimen of *C. kirkpatricki*. Two parallel, longitudinal, oval bosses on the opercula, mentioned by Harmer, are also present in your type-specimen. They are blister-like prominences on the outer surface of the operculum, and are conspicuous when the specimens (which are dry) are examined under a binocular microscope."

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SUBDIVISIONS OF THE GENUS *PTILINOPUS*

(AVES, COLUMBAE)

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A. J. CAIN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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LONDON: 1954

SUBDIVISIONS OF THE GENUS *PTILINOPUS*
(AVES, COLUMBAE)

ARTHUR JAMES CAIN
(Department of Zoology and Comparative Anatomy, University Museum, Oxford)

Pp. 265–284 ; 2 *Plates*

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SUBDIVISIONS OF THE GENUS *PTILINOPUS*
(AVES, COLUMBAE)

By ARTHUR JAMES CAIN

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SYNOPSIS

Previous arrangements of the species of *Ptilinopus* result in unnatural groupings. When one abandons the attempt to provide diagnoses for all groups, and gives due weight to the facts of geographical distribution, a far more natural classification can be constructed.

INTRODUCTION

THE genus *Ptilinopus* contains a large number of brightly coloured fruit-pigeons distributed from the Malay Peninsula, Philippines and Marianas to New South Wales, the Marquesas, and Henderson Island. Even within obviously natural groups of species of this genus so much interspecific variation occurs that it is almost impossible to find diagnostic characters. The last comprehensive review with diagnoses is that by Salvadori (1893) which, as was usual at that period, ascribes exaggerated importance to so-called anatomical characters. Some species have been reviewed by Rensch (1929), Mayr (1940), Ripley and Birckhead (1942) and Amadon (1943), but no general survey has appeared, except that Peters (1938) reviewed the limits of the genera of fruit-pigeons and gave diagnoses for those genera he recognized, together with a very brief survey of the interrelations of species within each genus. The checklist given by Peters (1937) is good for subspecific ranges and synonymy, but the arrangement of the species is unfortunate, several closely related forms being separated widely. Also, no indication is given of the limits of superspecies or species-groups.

The purpose of this paper is to present a classification of these pigeons, based on a study of the collections in the British Museum (Natural History). I am deeply indebted to Mr. J. D. Macdonald, who has given me every facility in examining the specimens, and to Mr. R. E. Moreau for advice and criticism.

PRINCIPLES

(1) *Recognition of natural groups*

If each of the members of a group of species is more closely related to some other members than to any species outside it, the group is natural; but it may well happen that every character that is confined to the group and therefore might be proposed as diagnostic is lost or modified in one or more species. If those species are clearly related by all their other characters to the rest of the group, they cannot be excluded from it.

This is the state of affairs found in the genus *Ptilinopus*. Consequently, the descriptions given below must be understood as indicating general characteristics, not as rigidly defining each subdivision. As Peters (1938) remarked of the subgenus *Ptilinopus*, it is very difficult to draw up a diagnosis that applies to all the species. I would add that it is unnecessary. When a natural group can be recognized but not diagnosed as such, it is sufficiently indicated by a description and a list of the contained species, as in the present paper.

When two species are clearly very closely allied but differ in one conspicuous character, it is obvious that in respect to these two species this character is only of specific importance. In another group, its distribution may coincide with that of so many other characters that it can be cited as characteristic of a genus, family, or group of even higher rank. The test of taxonomic importance of any character in a particular group is its distribution in that group with respect to all other characters.

This statement is true whatever the nature of the character—anatomical, physiological, embryological, genetical or ecological. The remark of Manuel (1936*b*) that " The subfamily Ptilopodinae is an artificial group for the reason that there are no trenchant structural characters peculiar to it " is consequently unacceptable. In some natural groups of birds the beak, feet, or structure of the feathers may show extraordinary variability while the colour pattern remains very constant; in others, the reverse is true. Consequently there is no need to assume *a priori* that in any group of birds structure is always more important taxonomically than colour-pattern. This was very nearly the assumption made by Salvadori (1893) as of course by most authors of that time. Consequently his keys almost always begin with an " anatomical " character (emargination of the first primary, length of the tail and wing, or strength of the beak). Unfortunately these characters are not invariably of the highest importance in *Ptilinopus* and its allies, and Peters (1938), although he implies (p. 376) that external structural characters are a *sine qua non* for erecting a subfamily (which may be true in practice but cannot be made into an absolute rule), remarks of *Ptilinopus* and its allies that " On the whole, colour in this group seems just as important, if not more so than structure." A survey of all the species, originally made without reference to Peter's paper, confirms his opinion.

(2) *Size*

The importance of any character, as was shown above, is determined only by its distribution in any particular group with respect to all other characters, and no one class of characters can be regarded on principle as always of greater taxonomic importance than any other.

Equally, no one class of characters can be considered on principle as always useless. Size tends to vary greatly in birds both between and within species, and is therefore not usually of much taxonomic value in groups above the level of the species. However, in the genus *Ptilinopus* size tends to remain comparatively constant in the species of some groups. The subgenera *Leucotreron* and *Ramphiculus* contain species which, for the genus, are rather or very large (wing-length 150–170 mm.). In the subgenus *Ptilinopus* all the members of the ornatus species-group ((10)–(14)) are rather large for this subgenus (wing-length 135–160 mm.), while those of the purpuratus species-group ((15)–(30)) with a solitary exception (*Pt. huttoni* (26)) are rather small (wing-length 95–145 mm.). Size is therefore included as a character in the descriptions of the groups. Within the genus as a whole wing-lengths of 90–139 mm. are considered small, 140–159 medium, and 160–170 large.

(3) *Keys and natural classifications*

Keys are constructed for the rapid identification of specimens. The characters employed are therefore those that are readily discernible, present in the largest possible number of individuals (not confined, for example, to a fleeting stage of development), least variable in their expression, and most easily defined verbally.

" Natural " classifications, on the other hand are constructed to display the general affinities and presumed evolutionary interrelationships of different forms. For this purpose characters totally different from those used in a key to the same group may be chosen, since the conspicuousness of a character bears no direct relationship to its taxonomic and phylogenetic importance. Yet monographs are still often burdened with " keys " which are designed to act both as guides to identification and as succinct accounts of a natural classification. In such " keys " it is common to find not only that the characters employed are often of little practical use for identification, but also that the necessity for defining each group by one or two characters may actually prevent the recognition of such natural groups as those described immediately above, which have no diagnostic characters. The reason why such " keys " are constructed is, of course, that by using them a new and undescribed form can usually be put into its natural group, whereas in a key made solely for identification it may very well be associated with widely differing species with which it happens to have some unimportant but conspicuous character in common. (For example, the character " bifid breast feathers " would bring together *Pt. porphyrea* (s.g. *Leucotreron*) and *Ducula goliath*, and most of the purpuratus species-group of *Ptilinopus*.) Nevertheless, the practice of combining both functions in the same key is not good. Together with the assumption that structure is always more important than colour, it was responsible for some of Salvadori's least successful groupings in *Ptilinopus*, as can be readily verified by anyone who will work through his classification. However, it is a striking tribute to Salvadori's genius that although he worked under these unnecessary limitations, his classification was by far the best produced until then, and most of his groups can still be regarded as natural.

(4) *Use of species-groups and subgenera*

Mayr (1942 : 290) has pointed out the great taxonomic advantages of the species-group. It is an informal natural group of closely related species, below the rank of a subgenus, the recognition of which involves no complication of the scientific names of the species contained in it. Moreover, having (unlike the subgenus) no formal name, it is not readily raised to the rank of a genus with a consequent change of the generic name throughout its component forms. In addition, in *Ptilinopus*, its use permits the recognition of natural groups of species without a general promotion of the subgenera to genera, and the genus perhaps to a subfamily. By using species-groups, the generic name can be retained throughout (which indicates the close relationship of the included species) while unmanageably large groups of species can nevertheless be broken up.

As the species-group is burdened by no formal rules there is no necessity to use the oldest valid name within a group as the name of that group. Consequently the group containing as its oldest named form the very atypical *Pt. tannensis* (14) can be called the ornatus group after a much more typical member (12). I have not changed the name of the purpuratus species-group (Ripley & Birckhead, 1942) because one should avoid nomenclatural disturbances wherever possible, and *Pt. purpuratus* (27), although a very simplified form, is certainly a member of the species-group that bears its name.

Although the subgenus has the disadvantage that it lengthens the names of its component forms in full citations, and is a standing temptation to reviewers to raise it to generic rank, it is nevertheless useful when, as in the genus *Ptilinopus*, many species-groups must be recognized but they fall clearly into two or more groups within the genus. Consequently it is used here to distinguish the three very natural groups which the genus *Ptilinopus* comprises. In smaller or less heterogeneous genera the species-group should be sufficient, without the use of subgenera.

(5) *The superspecies*

The superspecies (Mayr, 1942 : 169) is a monophyletic group of forms which replace each other geographically but are too diverse for all to be ranked as subspecies of a single species. The limit of permissible diversity cannot of course be specified, since in some groups good species are very similar, in others extremely diverse, so that in the former the diversity permissible among subspecies of a single species will be much less than in the latter, and forms with striking characters will be unhesitatingly separated as distinct species. Mayr (1942) gives examples of monophyletic arrays of geographical representatives in which some forms have even been segregated into a separate genus. Consequently a single superspecies may include only a few species of a single species-group, as in the occipitalis species-group ((4)–(7)), or all of them as in the lechlancheri species-group ((8)–(9)), or all of one species-group and one or more of another, as, for example, in the genus Halcyon (Mayr, 1942).

Consequently, the superspecies cannot strictly be used as a rank in the taxonomic hierarchy. However, when a series of geographically replacing forms is very heterogeneous there is usually some doubt as to whether it is really monophyletic, and it would be unwise, therefore, to list it as a superspecies. If there is no doubt, then most workers would consider that, since geographical variation is considerable in this series, the limits of subgeneric and generic variation in the natural group containing it should be wide. Consequently it would be given a low rank in the hierarchy. As a result it is rare to find a superspecies that transgresses the limits of a species-group, and in practice the superspecies can be regarded as a rank between the species and the species-group. The hierarchy of ranks used in the following classification is therefore :

- Genus,
  - Subgenus,
    - Species-group,
      - Subgroup (of species-group),
        - Superspecies,
          - Species.

CLASSIFICATION

The proposed classification is illustrated by the diagrams (Figs. 1 and 2) in which are represented all the species recognized by me. These diagrams are intended to demonstrate only the plumage pattern of each species. Relative size is not given and in each species the most highly ornamented subspecies and sex are shown (except in *Pt. rivoli* (32) and *solomonensis* (31) where there is very confusing convergence). Each species is given the same number in the diagrams as in the classification. Cross-hatching is used to represent shades of red, from orange to purple. All other colours are represented by stippling of appropriate darkness. Except for *Pt. merrilli* (5), specimens of all species and nearly all subspecies have been examined. The diagram of *Pt. merrilli* is based on the coloured plate of *P. m. faustinoi* given by Manuel (1936*a*), and on the descriptions by Delacour and Mayr (1946) and McGregor (1916). Full references to original descriptions of all forms will be found in Peters (1937) and Salvadori (1893).

(1) *Brief list*

- Genus *Ptilinopus*
  - Subgenus *Leucotreron*
    - *Pt. cincta* superspecies
      - *Pt. porphyrea* (1)
      - *Pt. dohertyi* (2)
      - *Pt. cincta* (3)
  - Subgenus *Ramphiculus*
    - (*a*) Occipitalis species-group
      - (i) Marchei subgroup
        - *Pt. marchei* (4)
        - *Pt. merrilli* (5)
      - (ii) Occipitalis subgroup
        - *Pt. occipitalis* superspecies
          - *Pt. occipitalis* (6)
          - *Pt. fischeri* (7)
    - (*b*) Leclancheri species-group
      - *Pt. leclancheri* superspecies
        - *Pt. leclancheri* (8)
        - *Pt. subgularis* (9)
  - Subgenus *Ptilinopus*
    - (*a*) Ornatus species-group
      - (i) Wallacii subgroup
        - *Pt. wallacii* (10)
        - *Pt. aurantiifrons* (11)
      - (ii) Ornatus subgroup
        - *Pt. ornatus* (12)
        - *Pt. perlatus* (13)
      - (iii) Tannensis subgroup
        - *Pt. tannensis* (14)
    - (*b*) Purpuratus species-group
      - (i) Superbus subgroup
        - *Pt. superbus* superspecies
          - *Pt. superbus* (15)
          - *Pt. perousii* (16)
      - (ii) Purpuratus subgroup
        - *Pt. monacha* (17)
        - *Pt. coronulatus* (18)
        - *Pt. pulchellus* (19)
        - *Pt. regina* (20)
        - *Pt. roseicapilla* (21)
        - *Pt. greyii* (22)
        - *Pt. richardsii* (23)
        - *Pt. porphyraceus* (24)

Pt. rarotongensis (25)
Pt. huttoni (26)
Pt. purpuratus (27)
Pt. insularis (28)
Pt. mercieri (29)
Pt. dupetithouarsii (30)

(*c*) Viridis species-group
(i) Rivoli subgroup

Pt. solomonensis (31)
Pt. rivoli (32)

(ii) Viridis subgroup

Pt. viridis (33)

(*d*) Hyogastra species-group
(i) Iozonus subgroup

Pt. iozonus superspecies
Pt. iozonus (34)
Pt. insolitus (35)

(ii) Hyogastra subgroup

Pt. hyogastra superspecies
Pt. hyogastra (36)
Pt. granulifrons (37)
Pt. naina (38)
Dubious member of this superspecies
Pt. melanospila (39)

(*e*) Jambu species-group

Pt. jambu (40)

(*f*) Lutovirens species-group

Pt. luteovirens superspecies
Pt. victor (41)
Pt. luteovirens (42)
Pt. layardi (43)

(2) *Detailed classification*

Genus *Ptilinopus* Swainson, 1825

Medium to small fruit-pigeons (wing-length 170 to 90 mm.) almost always with a plumage pattern including well-defined patches of colour forming conspicuous ornaments on the head and underparts, without a conspicuous yellow stripe on the wing, and with the first primary usually more or less clearly emarginate (falcate) at the distal end.

Subgenus *Leucotreron* Bonaparte, 1854 (Fig. 1).

Rather large Ptilinopids (wing-length about 160 mm.), with the head, neck, mantle and breast concolorous or simply patterned in bright colours and sharply marked off from the rest of the body by a narrow pale line followed on the ventral surface by a dark transverse bar. No tendency to ornamentation of the wings. First primary emarginate. Greater and Lesser Sunda Isles, Australia.

(1) *Pt. porphyrea* (Temminck, 1823). Sumatra, Java, Bali.
(2) *Pt. dohertyi* (Rothschild, 1896). Sumba.
(3) *Pt. cincta* (Temminck, 1810). Lesser Sunda Isles except Sumba, from Bali to Teun, Damar and Babar, and Northern Territory of Australia.

These three species are very closely allied, and if the very small overlap of *Pt. porphyrea* and *cincta* on Bali may be disregarded, they can be grouped as the *Pt. cincta* superspecies.

Subgenus *Ramphiculus* Bonaparte, 1854 (Fig. 1)

Medium-sized to large Ptilinopids (wing-length 150 to 170 mm.) with the most deeply coloured patches of the head-ornamentation (excepting the chin-stripe) lateral, sometimes meeting on the hind neck to form a ring. (A red cap occurs in *Pt. merrilli faustinoi*.) No tendency to ornamentation of the wings, nor to a pale line bounding the whole of the anterior parts as in *Leucotreron*. First primary emarginate, usually very obviously. Philippines and Celebes.

(*a*) Occipitalis species-group

Rather highly ornamented forms (plus one with a simplified pattern, *Pt. merrilli*), with a complex pattern on the head in which a chin stripe is not a well-marked feature, with breast and belly usually of different colours separated by a dark transverse abdominal line or band, and with spotted under tail coverts.

(i) Marchei subgroup

With a red cap and black auriculars, or only a cap, or no ornamentation on the head. Outer web of the secondaries composed of short widely separated red barbs.

(4) *Pt. marchei* (Oustalet, 1880). Philippines ; Luzon and Polillo.
(5) *Pt. merrilli* (McGregor, 1916). Philippines ; Luzon and Polillo.

(ii) Occipitalis subgroup.

With a red or black band joining the red auriculars across the nape. One superspecies.

(6) *Pt. occipitalis* G. R. Gray, 1844. Philippines.
(7) *Pt. fischeri* Brüggemann, 1876. Celebes.

(*b*) Leclancheri species-group

Rather plain species with a well marked dark chin-stripe, and plain (unspotted) brown under tail coverts. One superspecies.

(8) *Pt. leclancheri* Bonaparte, 1855. Philippines.
(9) *Pt. subgularis* Meyer and Wiglesworth, 1896. Celebes, Peling, Banggai and Sula Mangoli.

Subgenus *Ptilinopus*

Small to medium Ptilinopids (wing-length 90 to 160 mm. only in *Pt. huttoni* (26) 170 mm.), with strong tendencies to ornamentation of the wing coverts and scapulars and of the underparts, either a pectoral or abdominal patch or both being almost always present. The most deeply coloured patches on the head (excepting the chin stripe) are dorsal and median, forming a cap. First primary often clearly emarginate, sometimes obscurely so or merely tapering to the tip. Principally the New Guinea region and islands to the eastwards.

(*a*) Ornatus species-group

Forms rather large for this subgenus (wing length 135–160 mm.), highly ornamented (except for *Pt. tannensis* (14), an isolated form with a simplified pattern). Wing coverts spotted with pink, grey or white. There is a strong tendency to grey or olive yellow on the neck and breast. Abdomen plain green or with only a pale abdominal patch. Abdominal spot or bar (dividing the abdomen from the breast) always absent. Under tail coverts spotted. First primary not or only very slightly emarginate.

(i) Wallacii subgroup

With a red or orange cap, grey-spotted wing coverts, white chin and cheeks, and grey breast.

(10) *Pt. wallacii* (G. R. Gray, 1858). Babar, Timorlaut, Kei and Aru Isles.
(11) *Pt. aurantiifrons* (G. R. Gray, 1858). New Guinea, Western Papuan Islands, and Aru Isles.

(ii) Ornatus subgroup

With an olive-yellow cap (red in one subspecies), a grey chin, and olive-yellow breast. Wing coverts spotted with grey or bright pink.

(12) *Pt. ornatus* (Schlegel, 1871). New Guinea.
(13) *Pt. perlatus* (Temminck, 1835). New Guinea.

(iii) Tannensis subgroup

Head olive-yellow, most of the rest of the body plain green. Scapular spots white. Related to the ornatus subgroup.

(14) *Pt. tannensis* (Latham, 1790). New Hebrides and Banks Islands.

(*b*) Purpuratus species-group

Small to medium species (wing-length 95 to 145, 170 in *Pt. huttoni* (26)) with a bright red, purple or blue cap bordered behind with yellow (or with vestiges of such a cap), and with clearly or obscurely bifid breast-feathers. Scapular and wing-covert spots present, dark blue, pink, pale purple, or emerald green, often not clearly marked. Abdomen ornamented with a large patch and a darker transverse bar or spot, reduced or absent in a few forms. Under tail coverts plain red, orange or yellow (spotted only in *Pt. superbus*). First primary emarginate, almost always very clearly.

(i) Superbus subgroup

Lower neck and upper back with a more or less extensive bright brownish red or dark red band. Wide transverse abdominal band present. One superspecies.

(15) *Pt. superbus* (Temminck, 1810). Celebes and the Sulu Archipelago to the Solomons and eastern Australia.
(16) *Pt. perousii* Peale, 1848. Fiji, Tonga and Samoa.

(ii) Purpuratus subgroup

With no red on the lower neck and upper back, and no distinct humeral patch on the wing. With a narrow abdominal band transversely elongated (*Pt. pulchellus* (19)) or, much more frequently, a rounded or longitudinally elongated abdominal spot. One superspecies with two doublets (see p. 283).

(17) *Pt. monacha* (Temminck, 1824). North Moluccas (Halmahera, Ternate Batjan).
(18) *Pt. coronulatus* (G. R. Gray, 1858). New Guinea, Japen, Salawati and Aru Isles.
(19) *Pt. pulchellus* (Temminck, 1835). New Guinea and Western Papuan Islands.
(20) *Pt. regina* Swainson, 1825. Eastern and northern Australia, eastern Lesser Sunda Isles, Banda and Kei Isles.
(21) *Pt. roseicapilla* Lesson, 1831. Marianas.
(22) *Pt. greyii* Bonaparte, 1857. New Caledonia to Santa Cruz Islands and Gower Island.
(23) *Pt. richardsii* (Ramsay, 1882). Ugi, Santa Anna, and Rennell Island (Solomons).
(24) *Pt. porphyraceus* (Temminck, 1821). Fiji, Tonga, Samoa, Caroline and Palau Islands.
(25) *Pt. rarotongensis* Hartlaub and Finsch, 1871. Rarotonga.
(26) *Pt. huttoni* (Finsch, 1874). Rapa Island.
(27) *Pt. purpuratus* (Gmelin, 1789). Society Isles and Tuamotu or Lau Archipelago.
(28) *Pt. insularis* (North, 1908). Henderson Island.
(29) *Pt. mercieri* (Des Murs and Prévost, 1849). Nukuhiva and Hivaoa (Marquesas).
(30) *Pt. dupetithouarsii* (Neboux, 1840). Marquesas, widespread.

(*c*) Viridis species-group

Forms medium sized for this subgenus (wing-length 115–135 mm.). Pectoral patch large, sharply defined and coloured white, yellow, or deep red. Abdominal patch reduced and dark purple, or absent. Wing-covert spots present, dark blue or grey. First primary not or only very slightly emarginate.

(i) Rivoli subgroup

Wing spots dark blue. Abdominal patch present. Red or purple cap present, sometimes reduced to a pair of supraloral spots. Under tail coverts yellow.

(31) *Pt. solomonensis* (G. R. Gray, 1870). Solomon Islands, Bismarck Archipelago and some islands in Geelvink Bay.

(32) *Pt. rivoli* (Prévost, 1843). South Moluccas, Western Papuan Islands, north-west New Guinea, islands in Geelvink Bay, some islands off south-eastern New Guinea, Solomon Islands.

(ii) Viridis subgroup

Wing spots grey. Abdominal patch and red cap absent. Head shades of green and grey (rarely white). Size of pectoral patch varies greatly. Under tail coverts spotted.

(33) *Pt. viridis* (Linnaeus, 1766). South Moluccas, Western Papuan Islands, north-west New Guinea, islands in Geelvink Bay, some islands off south-eastern New Guinea, Solomon Islands.

(*d*) Hyogastra species group

Forms medium-sized to small for this subgenus (wing-length 90–130 mm.). Breast, neck and back plain green, unornamented. Abdomen with an orange or violet patch (absent in *Pt. melanospila* (39)). Head plain green or grey, unornamented or with a chin stripe and nuchal spot. First primary indistinctly emarginate or merely tapering.

(i) Iozonus subgroup

Head green with greyish ill-defined chin stripe. Abdominal patch large, orange. Grey patch on bend of wing, grey spots on wing-coverts. Under tail coverts spotted. One superspecies.

(34) *Pt. iozonus* (G. R. Gray, 1858). New Guinea, Western Papuan Isles and Aru Isles.

(35) *Pt. insolitus* (Schlegel, 1863). Bismarck Archipelago.

(ii) Hyogastra subgroup

Head grey (green in *Pt. naina*). Abdominal patch violet (absent in *Pt. melanospila*). Under tail coverts yellow, or yellow grading to red, not spotted. One superspecies. (Possibly *Pt. melanospila* should be kept separated.)

(36) *Pt. hyogastra* (Temminck, 1824). Halmahera and Batjan (North Moluccas).

(37) *Pt. granulifrons* Hartert, 1898. Obi Major.

(38) *Pt. naina* (Temminck, 1835). New Guinea and Western Papuan Isles.

(39) *Pt. melanospila* (Salvadori, 1875). Philippines, Celebes, Java, Lesser Sunda Isles (Bali to Alor) and Ceram.

(*e*) Jambu species group

Head red with black chin stripe. Upper parts green, underparts white with a pink flush on the upper breast and brown under tail coverts. First primary emarginate.

(40) *Pt. jambu* (Gmelin, 1789). Malay Peninsula, Sumatra, Borneo and islands between.

(*f*) Luteovirens species group

Rather small forms (wing-length about 115 mm.). Head more or less olive-yellow, rest of body almost uniform green, orange or yellow, with no colour-ornaments. Some contour feathers lax and hairy or bifid, or long and thickened. First primary not emarginate. One superspecies, confined to Fiji.

(41) *Pt. victor* (Gould, 1872). Vanua Levu, Taviuni, Kio Rambi, Ngamea, Lauthala.

(42) *Pt. luteovirens* (Hombron and Jacquinot, 1841). Viti Levu and nearby islands.

(43) *Pt. layardi* (Elliot, 1878). Kandavu and Ono.

NOTES ON THE CLASSIFICATION

(1) *Generic and subgeneric limits*

Peters (1938) divides the species considered in the present paper into three genera, *Leucotreron* (i.e., the subgenera *Leucotreron* and *Ramphiculus*), *Ptilinopus* (the subgenus *Ptilinopus* without the luteovirens species-group), and *Chrysoena* (the luteovirens species-group), which is divided into two subgenera. In this he differs from Salvadori only in promoting *Leucotreron* from a subgenus of *Ptilinopus*, and removing *Pt. jambu* (40) from it, in using no subgenera of *Ptilinopus* (Salvadori recognized twelve), and in accepting Wetmore's subdivision of *Chrysoena* (1925 : 833). Amadon (1943) has shown conclusively that *Chrysoena* must be ranked as a single superspecies (41–3), which requires no subdivision, of *Ptilinopus*. The separation of *Leucotreron* is justifiable since it differs sharply from the other groups recognized as subgenera of *Ptilinopus* by Salvadori, but when these are ranked only as species-groups, there is no good reason why *Leucotreron* should be generically separate. Moreover, as the classification given above will show, *Leucotreron* itself requires division. A glance at the diagrams indicates that the major division of the genus is into three, not two, groups, which have very different colour patterns and distributions ; accordingly, all three are recognized here as subgenera. This arrangement is the more satisfactory since the colour pattern of the subgenus *Leucotreron*, as recognized here, is so like that seen in both *Drepanoptila* (as Peters recognized) and in some of the most ornamented species of *Ducula*, that a complete revision of all the fruit pigeons may possibly show that *Leucotreron* should be separated generically from *Ramphiculus* and *Ptilinopus*.

The characters by which both Peters and Salvadori define their group *Leucotreron* (i.e., *Leucotreron* plus *Ramphiculus*) are the relatively long tail and the absence of a sharply-defined red or violet cap. Peters adds that the tarsus is feathered for more than half its length, there are no spots on the scapulars, tertials or wing coverts, and a humeral patch is absent, and refers *Pt. jambu* (40) not to *Leucotreron* but to *Ptilinopus*. In all these forms, the length of the tail tends to be associated directly with body size, which can vary considerably within a single species-group. The feathering of the tarsus is variable, but it is true that it is on the whole more extensive in both *Ramphiculus* and *Leucotreron* than in *Ptilinopus*. All the other characters are negative. Consequently, what *Ramphiculus* and *Leucotreron* share is mainly medium to large size and the absence of the distinctive characters of *Ptilinopus*. On such grounds as these it is difficult to see why *Ptilinopus* and *Leucotreron* should not be combined instead, in opposition to *Ramphiculus*, an arrangement which has never yet been proposed ; but even a cursory inspection of the positive characters of *Leucotreron* and *Ramphiculus* shows that all these subgenera must be separated.

The only species difficult to place is *Pt. jambu* (40), which shows an extraordinary mixture of characters. Because of its brown under tail coverts and black chin stripe Salvadori associated it with *Pt. leclancheri* (8) and *subgularis* (9), its emarginate first primary, lack of a cap, and rather long tail being sufficient to include it in his *Leucotreron*. Peters merely remarks that by his definitions it is a *Ptilinopus* (1938 : 378), but it is not easy to understand this remark, since his diagnosis of *Ptilinopus* is " tail less than seven-tenths of wing, often less than six-tenths, usually a trifle over six-tenths ; tarsus never feathered for more than three-quarters of its length, seldom over one-half ; a sharply-defined red or violet cap ; spots on scapulars, wing-coverts or tertials ; bend of wing often differently coloured from the back," while for his *Leucotreron* he gives " tail more than seven-tenths length of wing (usually more than 75 per cent.) ; tarsus feathered for more than half its length (usually from three-quarters to completely) ; no sharply-defined red or violet cap ; no spot on scapulars, wing coverts or tertials ; bend of wing concolour with back (no humeral patch)."

In fact, the curious distribution of red on the head of *Pt. jambu* could be derived either by extension of the red cap (and sometimes malar spots) of some *Ptilinopus* or by reduction of the pattern found in either *Leucotreron* or *Pt. marchei* (4). The chin stripe, unicolorous under tail coverts, pale underside, and lack of wing-ornaments are very reminiscent of *Ramphiculus* (the leclancheri species-group) but also, except for the pale underside, of *Pt. melanospila* (39) (*Ptilinopus*, hyogastra species-group). The distribution could be the result of a westward invasion from Celebes by either of these species-groups, or indeed of an extension from Borneo or Malaya by a geographical representative of *Pt. porphyrea*, producing a double invasion of Sumatra.

Garrod (1874) states that *Pt. jambu* (40), *Pt. perousii mariae* (purpuratus species-group (16)) and *Pt. melanospila melanauchen* agree in the structure of the gizzard and differ from *Treron calva*. Cadow (1933) who corrects and extends Garrod's observations, compared *Pt. cincta* (3), *porphyrea* (1) and *dohertyi* (2) (all *Leucotreron*) and *Pt. jambu* (40) with species of *Megaloprepia*, *Ducula*, *Treron*, *Columba*, and

Didunculus. He concluded that three main types of gizzard could be distinguished in the fruit pigeons, and that *Pt. jambu* agreed in this respect with the sub-genus *Leucotreron.* It seems, therefore, that the structure of the gizzard is much the same within the genus *Ptilinopus*, in the subgenera *Leucotreron* and *Ptilinopus*, and in *Pt. jambu*, and consequently gives no information about the position of *Pt. jambu.*

On the whole, the characters of *Pt. jambu* seem to me to suggest an association with *Pt. melanospila* (39) and thence with the rest of the subgenus *Ptilinopus*, but I have placed it in a species-group of this subgenus only with the greatest hesitation. It is most remarkable that the species situated geographically at the point of convergence of the ranges of the subgenera of *Ptilinopus* should show such a mixture of the characters of all three.

(2) Leucotreron *and* Ramphiculus

In discussing the species of these two subgenera Peters (1938 : 378) was misled by the bifid breast feathers of *Pt. porphyrea* (1) and the rich red on its head and breast into considering it most closely allied to the subgenus *Ptilinopus*, and to *Pt. occipitalis* (6) and *Pt. marchei* (4), the most ornamented members of *Ramphiculus.* Consequently he proposed an artificial arrangement beginning with *Pt. porphyrea* (1), followed by the occipitalis species-group (4–7), then the leclancheri species-group (8–9), and finally *Pt. cincta* (3) and *dohertyi* (2) which he regarded as highly specialized. " The more I study *cinctus* and *dohertyi*," he writes, " the more apparent it becomes that these two species are the most specialized members of the genus [his *Leucotreron*] ; it is also evident that in spite of their superficial dissimilarity to each other in colour, they are certainly derived from the same ancestral stock, the densely feathered tarsi, proportion of wing to tail, modification of the inner primaries and the pale anterior part of the body sharply defined from the dark posterior, all point to some common ancestor." His failure to associate them with *Pt. porphyrea* in spite of these very apposite remarks is in agreement with the fact that in the Checklist (1937) he arranged the members of the purpuratus species-group in a very similar and artificial way, bringing together the most highly ornamented forms with no regard for the geographical evidence.

Bifid breast-feathers occur independently (as Peters points out, p. 388) in several groups of pigeons, including (to take examples only from the fruit-pigeons) species of the purpuratus species-group and luteovirens species-group in the subgenus *Ptilinopus*, and *Ducula goliath.* They vary much in degree of development even among closely related forms ; even if they do represent the retention of an ancestral character, it is evident that the common ancestor possessing them must be a long way back in the lineage of the pigeons. Certainly those species that possess them to-day are not closely related. The whole pattern of ornamentation of *Pt. porphyrea* links it not with the subgenera *Ramphiculus* or *Ptilinopus*, but with *Pt. dohertyi* and *Pt. cincta.*

Even if richness of ornamentation can be considered as one " character," it is not a useful character in this genus since it has evidently been lost (or perhaps gained) independently several times, as shown in the following table :

Ornamentation in Closely Allied Species

Species-group.	Complex.	Simple.
Occipitalis	*Pt. marchei* (4)	*Pt. merrilli* (5)
	Pt. occipitalis (6)	*Pt. fischeri* (7)
	Pt. leclancheri (8)	*Pt. subgularis* (9)
Ornatus	*Pt. ornatus* (12) and *perlatus* (13)	*Pt. tannensis* (14)
Purpuratus	*Pt. superbus* (15)	*Pt. perousii* (16) (see Cain, 1954)
	Pt. regina (20)	*Pt. purpuratus* (27) and geographically adjacent forms.

The luteovirens species-group (41–3) also consists entirely of a group of long-isolated forms with extremely simple patterns derived from the subgenus *Ptilinopus* (Amadon, 1943) which contains principally highly ornamented forms. Variation between a complex and a more simple pattern has therefore occurred at least seven times independently in the genus (and certainly involves a simplification in three examples). But, more important, " richness of ornamentation " as a character is clearly applicable to species which agree only in that they are richly ornamented and differ profoundly in their patterns of ornamentation. *Pt. porphyrea* (1), *marchei* (4) and *superbus* (15), for example, are all richly ornamented, but their affinities are not with each other but with *Pt. dohertyi* (2), *merrilli* (5) and the purpuratus species-group (15–28) respectively ; to class them together on the basis of this very superficial " character " is to ignore entirely the wealth of evidence on their real affinities provided by their pattern of ornamentation. Colours often vary greatly in intensity between subspecies, still more between species, but the pattern tends to remain constant in most species-groups. There is no doubt that the pattern of *Pt. porphyrea* (1) links it with *Pt. dohertyi* (2) and *Pt. cincta* (3).

The three species of *Leucotreron* are geographical representatives except for a single overlap on Bali, and can be regarded as a single superspecies. The loss of bright red pigment in the Lesser Sunda Isles form (*Pt. cincta* (3)) is paralleled by the reduction of red and yellow in the subspecies of *Pt. regina* (20) (purpuratus species-group) in the same area. No other species of the genus *Ptilinopus* is found, in these islands except *Pt. melanospila* (39), which is obviously a very recent arrival from Celebes.

The species of *Ramphiculus* fall naturally into two ecological groups, the marchei subgroup (4–5) being confined to mountain forest in the Philippines (Delacour and Mayr, 1946), while *Pt. occipitalis* (6) and *lechlancheri* (8) are lowland-forest species both of which have colonized Celebes and produced there simplified forms with no ornamentation on the breast and belly.

(3) *Subgenus* Ptilinopus

This subgenus can be readily subdivided into five species-groups, characterized by the accentuation of different elements of the pattern. In the ornatus group there is considerable ornamentation of the wing-coverts and head, but very little on the lower breast and belly. In the purpuratus group the cap, breast-patch, abdominal band or spot, and abdominal patch are conspicuous. In the viridis group the breast-patch is greatly accentuated, and in the hyogastra group the abdominal patch. The luteovirens species-group (41–3), like *Pt. perousii* (16) (Cain, 1954) shows a simplified pattern, as is usual in members of reduced avifaunas.

Strong sexual dimorphism is found sporadically in the subgenus *Ptilinopus* (but in the other subgenera only in *Pt. leclancheri* (8)) and requires discussion in relation to specific limits. It occurs in the ornatus group only in *Pt. tannensis* (14) (Amadon, 1943). In the purpuratus group it is present in both members of the superbus subgroup, and in *Pt. monacha* (17), which is otherwise very closely related to *Pt. coronulatus* (18). In the hyogastra group dimorphism is slight or absent except in *Pt. melanospila* (39) in which the female has a green head. It is also seen in *Pt. jambu* (40) in which the red of the head is much duller in the female and there is some green on the breast. In the viridis group strong dimorphism is usual, but it varies greatly in the various subspecies of *Pt. viridis* (33). In this species there is a red breast-patch, which is large in *Pt. v. viridis* (southern Moluccas) and present in both sexes although perhaps very slightly smaller in the females. In *Pt. v. pectoralis* (western Papuan Islands and north-west New Guinea) it is very small in the males and absent in the females. In *Pt. v. salvadorii* (Japen and the adjacent part of northern New Guinea) it is rather larger and is present, though reduced, in the females. In fact it appears that in these subspecies the patch is always smaller in the females than in the males and when it is very reduced in the males it is necessarily absent in the females. But in *Pt. v. geelvinkianus* (some islands in Geelvink Bay) it is large in the males and quite absent in the females. In *Pt. v. vicinus* (D'Entrecasteaux Archipelago and Trobriand Isles), *Pt. v. lewisii* (Lihir Islands and most of the Solomons), and *Pt. v. eugeniae* (San Christobal) it is quite large in both sexes.

Because of this variation in dimorphism, Peters divides *Pt. viridis*, as understood here, into four species, *Pt. viridis*, *eugeniae* (including *lewisii* and *vicinus*), *geelvinkiana*, and *pectoralis* (including *salvadorii*). This is not necessary. All these forms are very closely related and all are geographical representatives, with no overlap or contiguity of ranges. Consequently, since they never meet in the wild, it is impossible to say whether they are species or subspecies ; when there is reasonable doubt it is much more convenient to list such forms as subspecies, so that their close relationship is immediately obvious from their names. Sexual dimorphism is not necessarily a specific character. It is an individual character varying within single populations in some of the Geospizinae (Lack, 1947).

(4) *The purpuratus species-group*

This species-group is the largest and the most difficult to subdivide in the genus. It has been revised recently by Ripley and Birckhead (1942) who have introduced many notable improvements in the arrangement of the various forms. A further consideration of it (Cain, in press) shows that certain alterations to Ripley and

Birckhead's subdivisions are necessary. They omit *Pt. pulchellus* (19) and *Pt. superbus* (15) which also belong to the group (Cain, 1954), and divide the forms into four subgroups, (i) the " old stock," the forms in Australia, New Guinea the North Moluccas, and the Marianas (17, 18, 20, 21), (ii) Subgroup A, the forms from Rarotonga eastward and *Pt. perousii*, (16, 25–28), (iii) Subgroup B, those in the Solomons, New Hebrides, Fiji (*Pt. porphyraceus*), Carolines and Palau Islands (22–24) and (iv) the two Marquesan forms (29, 30) which they think should probably be placed in Subgroup B. The characters given by them as distinctive of Subgroups A and B are inconstant. They were unfortunately unable to see specimens of *Pt. rarotongensis* (25). An examination of specimens in the British Museum (Natural History) shows that it is in every way intermediate in pattern as well as geographically between *Pt. porphyraceus* (24)) (Subgroup B) and *Pt. purpuratus* (27) (Subgroup A), and that the proposed distinction between the two subgroups cannot be upheld. On the basis of this distinction, Ripley and Birckhead suggest that the " old stock " has given rise to two eastward expansions, one producing Subgroup A including *Pt. perousii* (16), the other Subgroup B, to the west of A, which has since spread into Fiji (*Pt. porphyraceus* (24)) and there overlaps with Subgroup A without interbreeding. Subgroup B, they suggest, has also colonized the Marquesas twice (producing *Pt. dupetithouarsii* (30) and *Pt. mercieri* (29)), leaping over the enormous range of Subgroup A to do so.

The abolition of the distinction between Subgroups A and B allows us to recognize that, with the exception of *Pt. perousii* (16) and the Marquesan species (29, 30) all the forms from *Pt. regina* (20) eastward are geographically representative and so closely allied that there is no reason to believe them to be more than the results of a single vast eastward expansion (Cain, in press). *Pt. perousii* (16) does not belong to this superspecies, but forms with *Pt. superbus* (15) a distinct subgroup within the species-group (Cain, 1954). The closest allies of the Marquesan species are *Pt. insularis* (28) on Henderson Island (regarded by Ripley and Birckhead as a subspecies of *Pt. purpuratus* (27)) which appears to be closely related to *Pt. mercieri* (29), and *Pt. purpuratus* (27) which is allied to *Pt. dupetithouarsii* (30). There is no doubt (Mayr, 1940) that the Marquesan species are the result of a double invasion by the same stock. Both, consequently, are geographical representatives of their closest allies, but it is not possible to choose one rather than the other to add to the superspecies, leaving one outside it because of their overlap. Consequently in the classification given above they are placed next to their closest allies and bracketed together as a *doublet*. The same procedure is used for *Pt. pulchellus* (19) and *Pt. coronulatus* (18) for the same reason. The whole of the purpuratus subgroup can then be accurately described as one superspecies with two doublets.

The Henderson Island form, *Pt. insularis* (28) although a geographical representative of all the others in the subgroup, is probably rather more closely allied to a member of the Marquesan doublet (namely *Pt. mercieri* (29)) than to any of the non-overlapping forms. But its relationships are so complex that it is retained here as a single species, since it could probably be considered almost equally well as a subspecies of either *Pt. mercieri* (27) or *Pt. purpuratus* (27). Whatever its detailed relationships, it is certainly a member of the superspecies.

SUMMARY

1. Proposed classifications of the large genus *Ptilinopus* are unsatisfactory, because either they are constructed on the principle that anatomical characters are invariably more important than colour-pattern, or they are really keys. A classification considered to be free from these defects is given.

2. Because of considerable variation in specific characters, it may be impossible to diagnose a very natural group of species. The group is then sufficiently defined by a description of its principal trends of variation, and a list of its contents.

3. Examples are given of the use of the species-group as a convenient informal taxonomic rank, indicating relationships without causing nomenclatorial upheavals.

4. The use of brackets for indicating multiple invasions by closely related stocks is exemplified.

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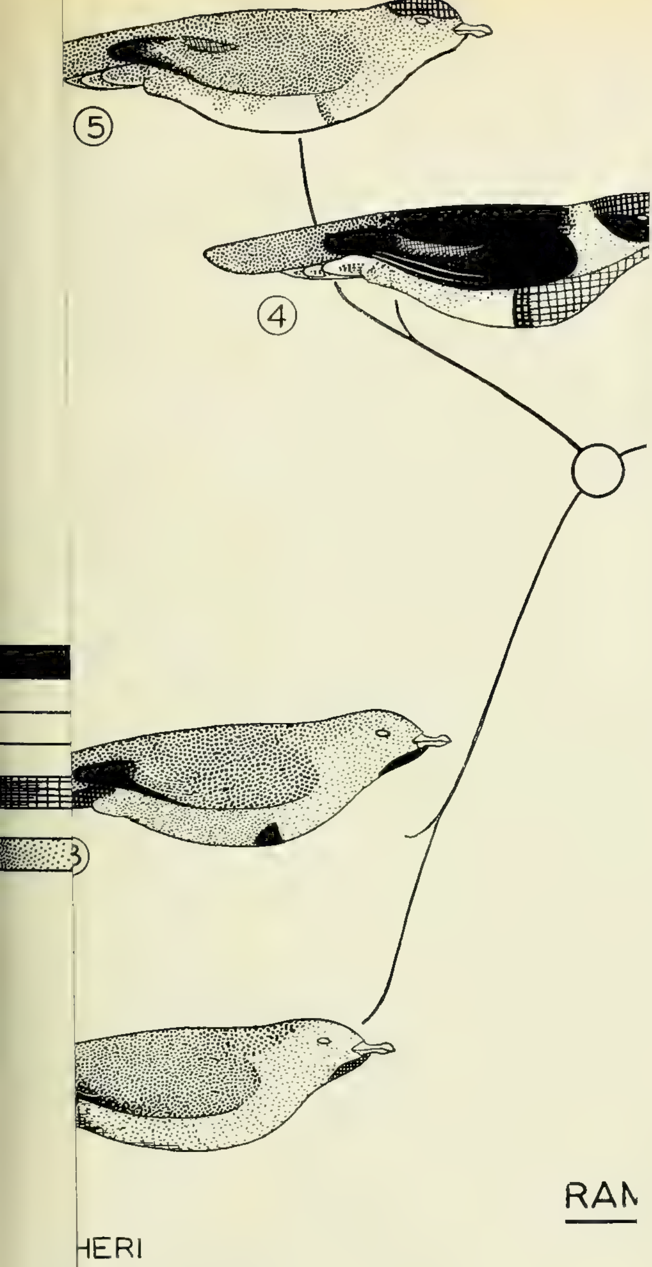
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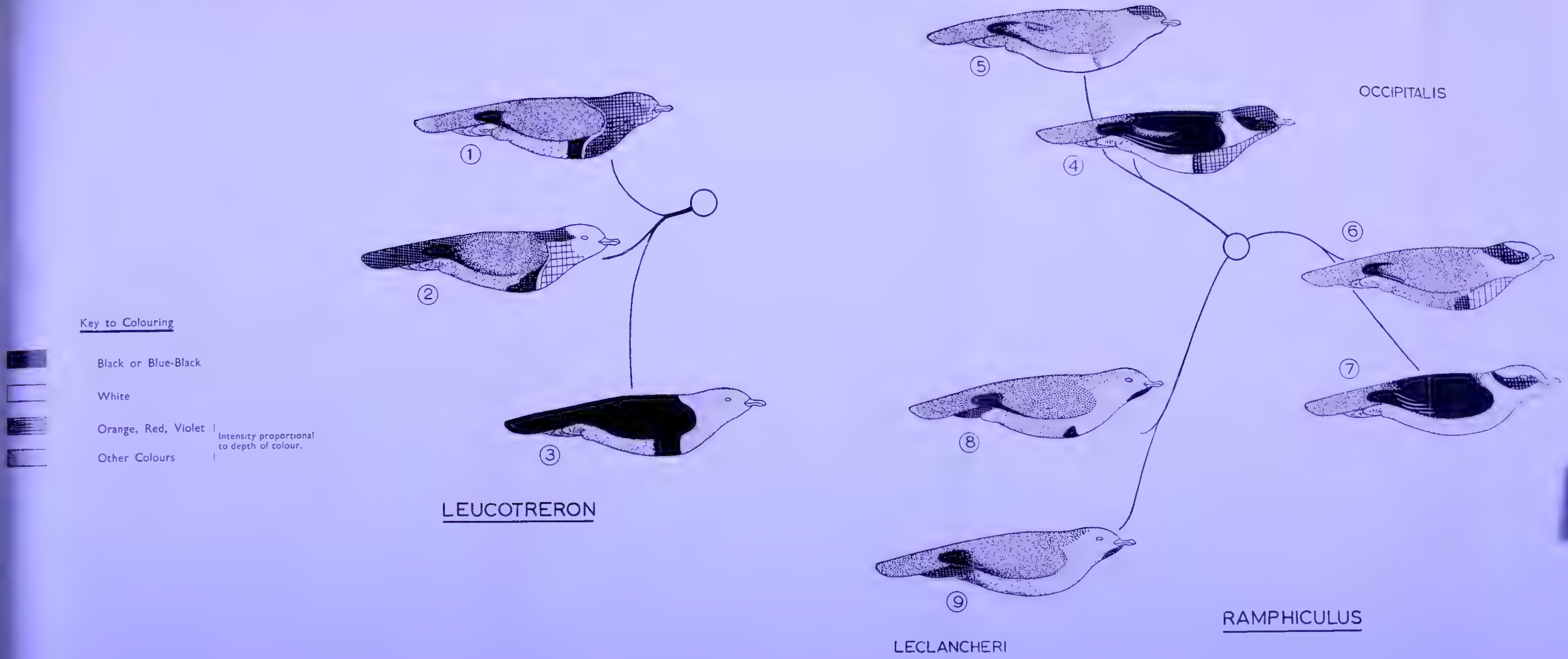
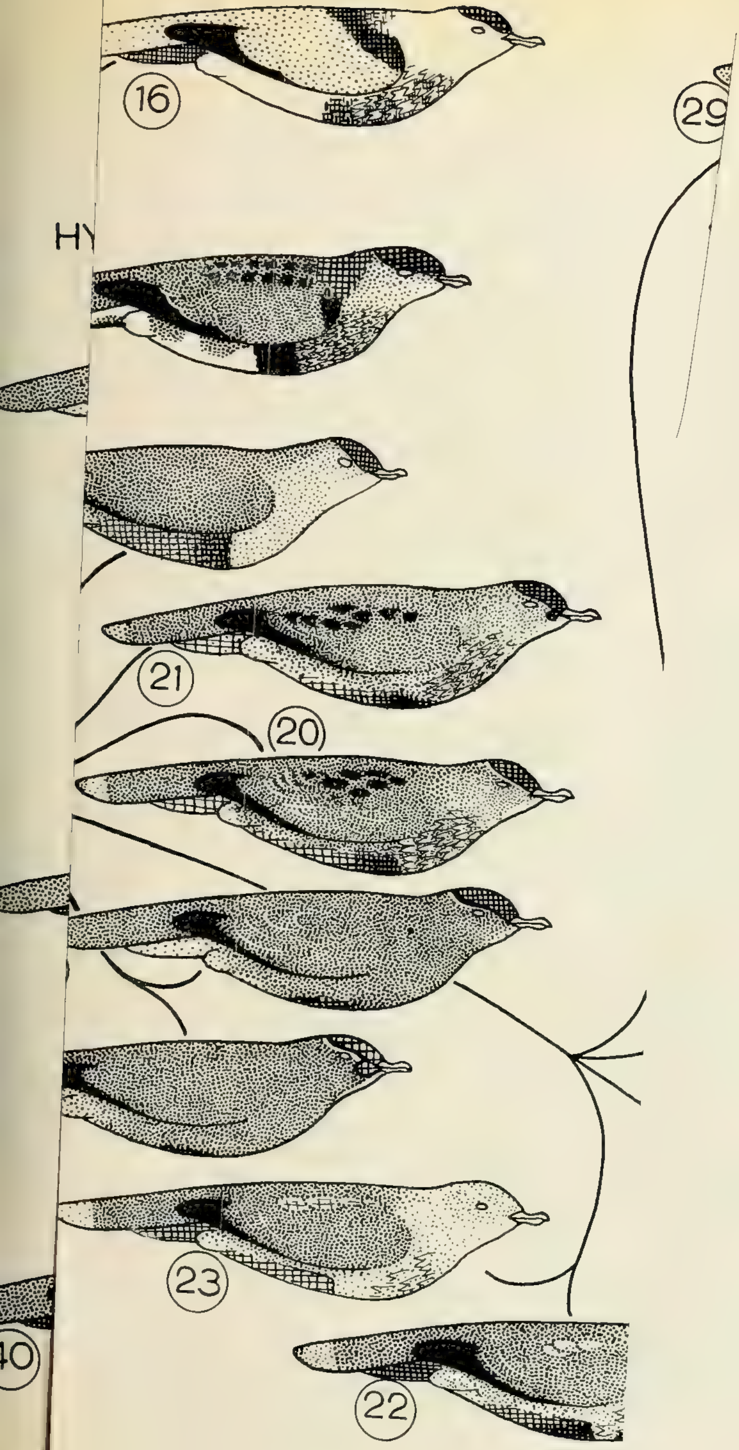

Key to Colouring
Black or Blue-Black
White
Orange, Red, Violet
Other Colours
Intensity proportional to depth of colour.
①
②
③
LEUCOTRERON
⑤
OCCIPITALIS
④
⑥
⑦
⑧
⑨
RAMPHICULUS
LECLANCHERI

Fig. 1.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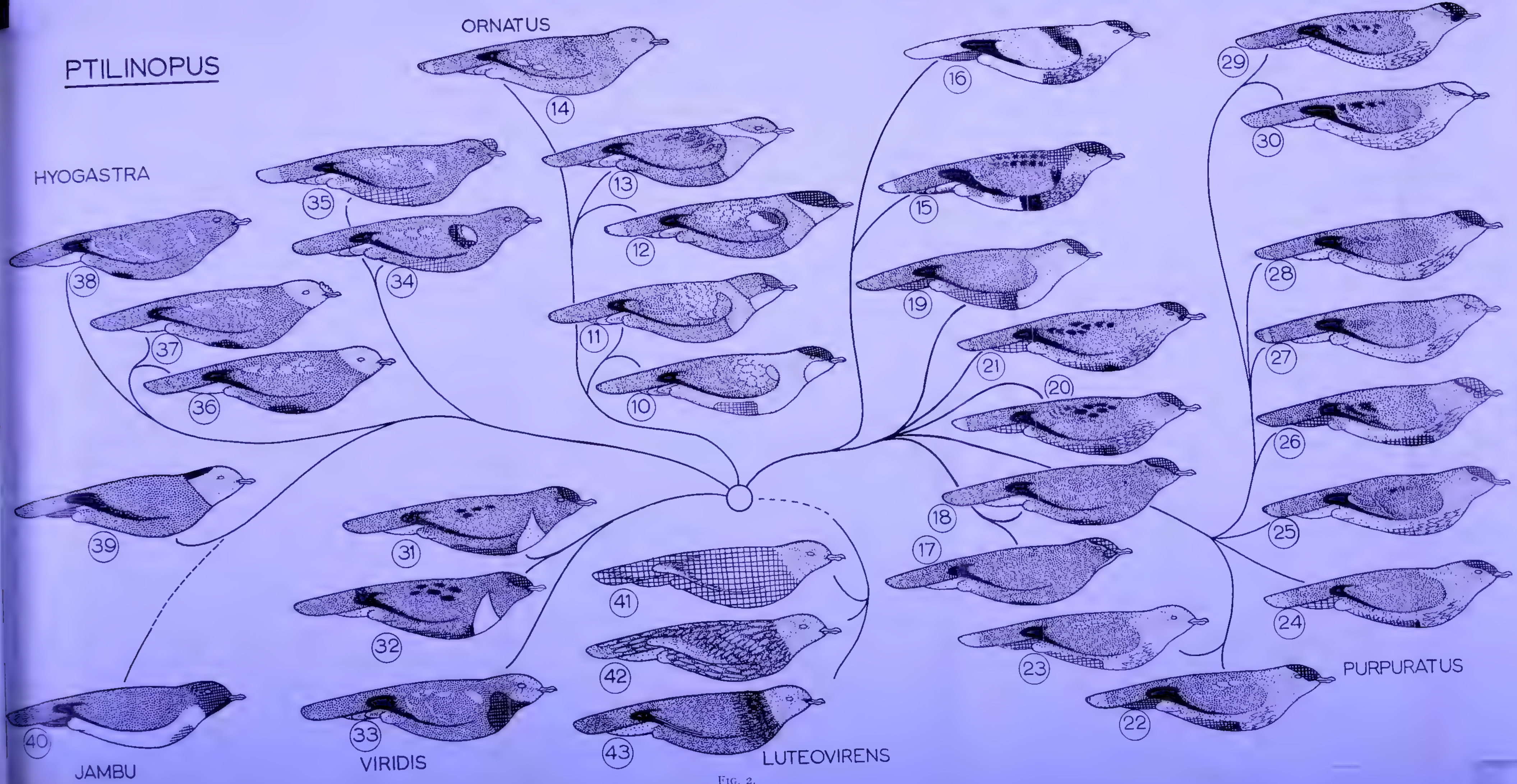
PTILINOPUS
ORNATUS
HYOGASTRA
JAMBU
VIRIDIS
LUTEOVIRENS
PURPURATUS

Fig. 2.

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A COLLECTION OF MESOSTIGMATID MITES FROM ALASKA

By G. OWEN EVANS

SYNOPSIS

One new genus and six new species are described; the classification of the Epicriina is discussed and a new family ARCTACARIDAE is erected; the Arctic species (females only) of the genus *Arctoseius* Thor are keyed.

INVESTIGATIONS on the acarine fauna of the Arctic prior to 1904 have been summarized by Trågårdh (1904). Since this date a number of papers on the systematics and ecology of Arctic mites has appeared particularly on the Oribatei. The most important contributions to the study of the Mesostigmatid mite fauna have been made by Trågårdh (1910), Thor (1930), Sellnick (1940) and Haarløv (1942).

The present work deals with part of a collection of mites from Alaska deposited in the collections of the British Museum (Nat. Hist.) by the collector, N. A. Weber, in 1950. A preliminary account of the fauna and descriptions of the habitats from which collections were made has been published by Weber (1950). Of the seven species of Mesostigmatid mites present in the collection six are described as new to science including one new genus and one new family.

The type material is deposited in the British Museum (Nat. Hist.).

MESOSTIGMATA—GAMASINA

Family LAELAPTIDAE Berl., 1892.

Haemogamasus alaskensis Ewing, 1925

1925. *Haemogamasus alaskensis* Ewing, H. E., Proc. biol. Soc. Washington **38** : 138–139.
1933. *Haemogamasus sternalis* Ewing, H. E., Proc. U.S. Nat. Mus. **82** : 3.

The type specimen, a single female, was collected on a *Microtus* sp. at Crater Mountain, Ophir, Alaska. It is also known from a number of localities in United States of America (Keegan, 1951).

The collection under study contained numerous females and nymphs from Point Barrow.

Family PHYTOSEIIDAE Berl., 1913

Genus ***Arctoseius*** Thor

1930. *Arctoseius* Sig. Thor, Skr. Svalbard Ishavet Oslo, **27** : 112.
1948. *Tristomus* Hughes, A. M., Mites associated with stored food products, H.M.S.O., London : 138–139, *syn. nov.*

The genus *Arctoseius* was erected by Thor (1930) for *Arctoseius laterincisus* Thor (1930), a mite collected under stones on the island of Spitzbergen. The original description and photographs of the genotype are unfortunately inadequate for its precise identification. Haarløv (1942) published a redescription, with figures, of what he considered to be *A. laterincisus* from material collected in Greenland. Thor and Haarløv's species are undoubtedly congeneric but without examining the type material of the former it is not possible to be certain that they are conspecific. For the present, however, the writer accepts Haarløv's interpretation of Thor's species.

In 1948, Hughes erected a new genus, *Tristomus*, which is closely related to *Arctoseius* in the structure of the venter of the female, the epistome and gnathosoma. Recently the writer remounted and examined the genotype, *Tristomus butleri* Hughes, and found that the dorsal shield in both sexes has lateral incisions characteristic of *Arctoseius*; the species should be removed to that genus.

The most comprehensive study of the genus *Arctoseius* to date was made by Willmann (1949) who added seven species to the genus; six of which were new to science. Willmann also proposed the division of the genus into four subgenera, namely, *Arctoseius* s. str., *Arctoseiulus*, *Arctotarseius* and *Arctoseiodes*. The subgenus *Arctoseiodes* (type *Arctoseius* (*Arctoseiodes*) *ibericus* Willm. (1949) is characterized by females having a ventri-anal shield and a genital shield with a pair of setae. It is sufficiently distinct from the *Arctoseius* group to warrant generic status. The subgenera *Arctoseiulus* (type *Laelaps* (*Iphis*) *semiscissus* Berl.) and *Arctotarseius* (type *A.* (*Arctotarseius*) *austriacus* Willm.) are separated from *Arctoseius* s. str. by the occurrence of a pair of jugular plates in the former and the structure of tarsus I in the latter.

Vitzthum (1941) placed *Arctoseius* in the Hypoaspidinae, but as Willmann (1949) has pointed out, the genus is more closely related to the *Lasioseius*-group. The subfamily Podocininae into which Willmann (loc. cit.) transferred the genus contains as its type genus *Podocinium* Berl., a typical Macrochelid. *Arctoseius* should be placed in the Phytoseiinae (family Phytoseiidae).

The following is an emended definition of the genus *Arctoseius*:

Small free-living mites with the entire dorsal shield incised laterally. Dorsal shield with 31 pairs of simple setae, lateral interscutal membrane with 10 pairs of setae. Ventral surface of female with a narrow genital shield without setae and pores. Sternal shield with two or three pairs of setae. Metasternal setae may or may not be situated on small platelets. Anal shield well separated from the genital. Peritrematal plate usually fused with dorsal shield anteriorly but may be free in those species showing a reduction in the peritreme. In the male the sterniti-genital shield is distinct from the large ventri-anal shield. The gnathosoma is normal for the family. The chaetotaxy of the palptrochanter, femur and genu is (2–5–6). The epistome is bi- or tridentate. All the legs are provided with a pulvillus and two claws. Genotype, *Arctoseius laterincisus* Thor (1930).

The Arctic species (females only) of *Arctoseius* s. str. may be separated as follows:

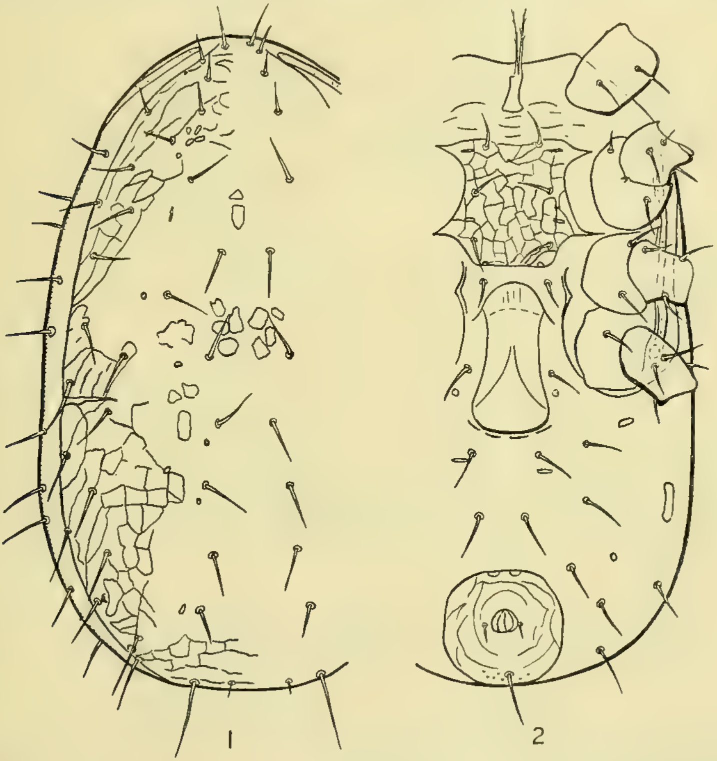
1. Tarsus I with a conspicuous sensory organ laterally *Arctoseius laterincisus* (Thor) Haarløv, 1942.
–. Tarsus I without such sensory organ laterally . . . . 2.

2. Epistome bidentate . . . . *Arctoseius cetratus* (Sell), 1940.
–. Epistome tridentate . . . . 3.
3. Peritreme extending beyond the level of coxa I . . *Arctoseius ornatus* sp. nov.
–. Peritreme reduced, not reaching coxa I . . . . 4.
4. Movable digits of chelicerae about 3 times as long as the corniculi, para-anal setae about ½ length of the post-anal seta . . *Arctoseius weberi* sp. nov.
–. Movable digits of chelicerae about 1½ times as long as the corniculi, para-anal setae approximately equal in length to the post-anal seta *Arctoseius multidentatus* sp. nov.

A. laterincisus has been recorded from Spitzbergen (Thor, 1930) and Greenland (Haarløv, 1942). The type locality of *A. cetratus* (syn. *Arctoseius bispinatus* Weis Fogh, 1947) is in Iceland. This species has also been recorded from Denmark and England under *A. bispinatus*.

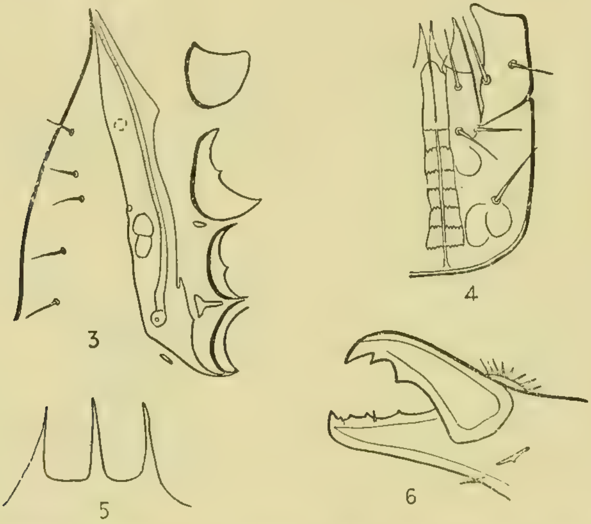
Arctoseius ornatus sp. nov.

Female. The dorsal shield is strongly ornamented and bears 31 pairs of simple setae distributed as in Fig. 1. The lateral incisions of the shield are distinct. The interscutal membrane surrounding the shield is provided with ten setae laterally.



FIGS. 1–2. *Arctoseius ornatus* sp. nov., female. Fig. 1, dorsal view. Fig. 2, ventral view.

Ventrally, the heavily ornamented sternal shield has the normal three pairs of setae and their associated pores (Fig. 2). The anterior margin of the shield in the paratype is indentated between the first pair of sternal setae. The posterior margin is truncated. The third pair of sternal pores normally associated with the metasternal setae are situated on the posterior margin of the sternal shield. The metasternal setae are not borne on platelets. The genital shield is narrow with its posterior margin slightly convex. The endopodal plates in the region of coxae III and IV are poorly developed. The genital setae and associated pores are situated lateral to it. The post-epigynial plates are four in number. The region between the genital and the anal shield is furnished with ten setae and four small platelets. The metapodals are elongate. The remaining four ventral setae are placed lateral to the anal shield—two on each side. The anal shield is almost circular in contour (102 × 99μ) and bears the normal three setae. The para-anal setae are less than one-half the length of the post-anal seta.



FIGS. 3–6. *Arctoseius ornatus* sp. nov., female. Fig. 3, lateral view. Fig. 4, Gnathosoma ventral. Fig. 5, tectum. Fig. 6, chelicera.

The stigmata are situated ventro-laterally in the region of coxa IV. The peritreme is well developed and reaches beyond coxa I (Fig. 3). The peritrematal plate is relatively large for the genus and is fused anteriorly with the dorsal shield. Posteriorly it extends a short distance around the posterior margin of coxa IV. The exopodal plates are fragmentary and not fused with the peritrematal.

The tritosternum is normal for the genus. The ventral surface of the gnathosoma is provided with four pairs of setae distributed as in Fig. 4. The ventral groove is provided with seven rows of denticles. The corniculi are short and do not extend beyond the anterior margin of the palptrochanter. The pedipalps are normal and the chaetotactic formula for the first three free segments is (2–5–6). The specialized seta on the palptarsus is two-pronged. The tectum (epistome) is tridentate (Fig. 5).

The chelicerae are strongly formed (Fig. 6). The movable digit is bidentate and the fixed quadridentate with a short pilis dentilis.

All legs are normal for the genus.

DIMENSIONS. Length 490–528μ, breadth 280–285μ.

LOCALITY. Two females from Point Barrow, Alaska (*Coll. A. Weber*, 1950); holotype (1954.3.19.8) and paratype (1954.3.19.9).

Arctoseius weberi sp. nov.

FEMALE. The dorsal shield is faintly reticulated. The chaetotaxy of the shield and the lateral interscutal membrane is normal for the genus.

Ventrally, the anterior and posterior margins of the ornamented sternal shield are indentated (Fig. 7). The shield bears three pairs of setae and three pairs of pores; the third pair of sternal pores being situated in its posterior margin. The prae-endopodal shields, although weakly sclerotized, are relatively large. The metasternal setae lie posterior to the shield. The endopodal plates are weak. The flask-shaped genital shield is faintly sculptured and covered with minute punctures. The genital setae and pores lie off the shield. The post-epigynial and endopodal shields are well-formed. The eight pairs of ventral setae are distributed as in the figure. The anal shield is broader than long (80 × 98μ). The para-anal setae are about one-half the length of the post-anal setae.

The stigma is situated ventro-laterally between coxae III and IV. The peritreme is reduced and reaches just beyond the anterior border of coxa II (Fig. 8). The peritrematal plate is strongly formed but not fused with the dorsal shield as in the preceding species. The exopodals are fragmentary and not fused with the peritrematal plate.

The tritosternum is normal for the genus and the gnathosoma is basically similar to that of the preceding species (Fig. 9). The corniculi are approximately one-third the length of the fixed digit of the chelicerae. The pedipalps are normal. The specialized seta on the palptarsus has two prongs. The tectum (Fig. 10) is tridentate with the median prong divided into three short processes distally.

The movable digit of the chelicera is bidentate and the fixed multidentate with a short *pilis dentilis* (Fig. 11).

All legs normal for the genus.

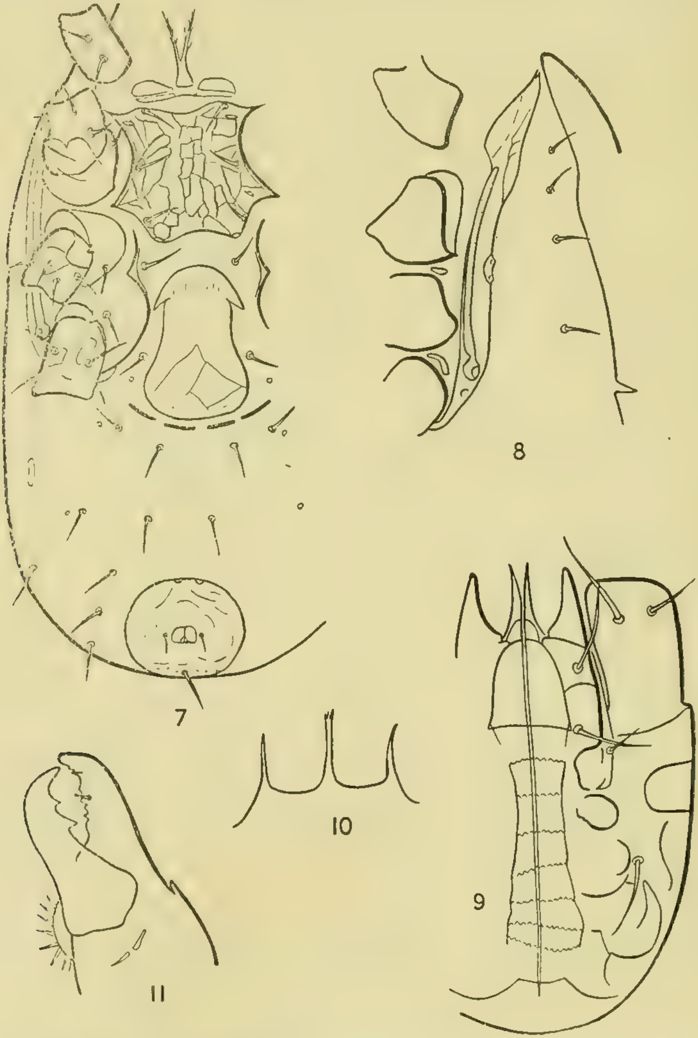
DIMENSIONS. Length 540μ, breadth 286μ.

LOCALITY. A single female (the holotype 1954.3.19.10) from Point Barrow, Alaska (*Coll. A. Weber*, 1950).

Arctoseius multidentatus sp. nov.

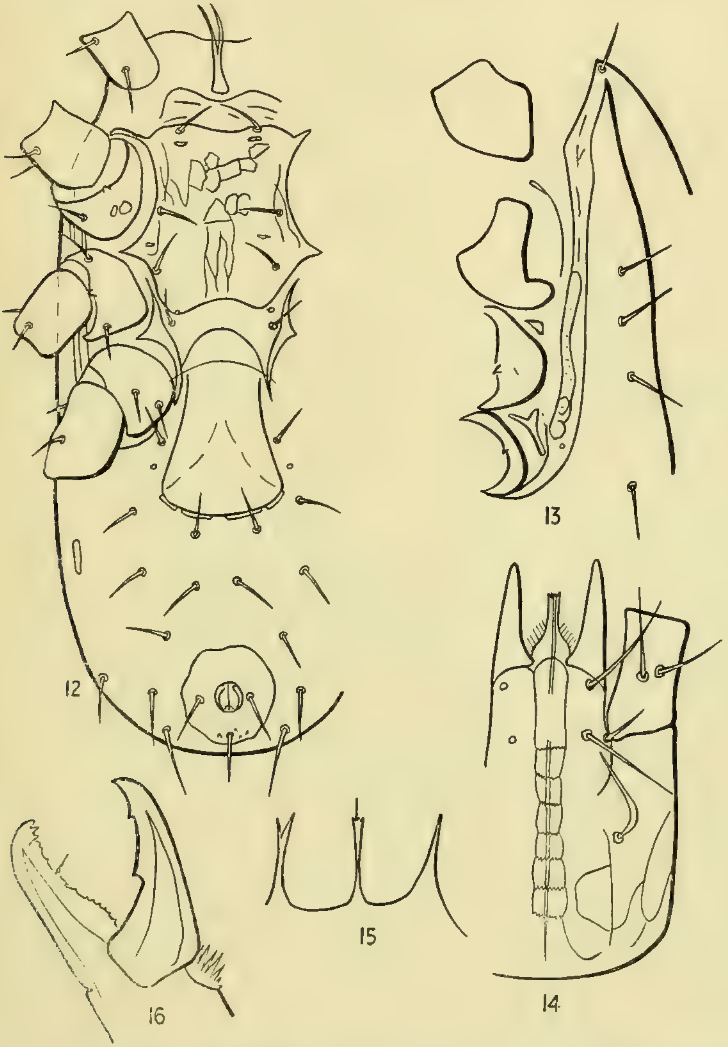
The form and chaetotaxy of the dorsal shield is similar to the preceding species. The lateral interscutal membrane bears the normal ten pairs of setae.

Ventrally, the sternal shield is lightly ornamented ; the ornamentation being strongest in the median region of the shield (Fig. 12). The three pairs of sternal setae are normal in position as are the two anterior pairs of pores. The third pair of pores is unusual, perhaps aberrant, in that one is situated on the sternal shield while the other is located on the interscutal membrane between the posterior-lateral



FIGS. 7–11. *Arctoseius weberi* sp. nov., female. Fig. 7, ventral view. Fig. 8, lateral view. Fig. 9, gnathosoma ventral. Fig. 10, tectum. Fig. 11, chelicera.

margin of the dorsal shield and the metasternal seta. The region anterior to the sternal shield is lightly sclerotized but not differentiated into prae-endopodal shields as in the preceding species. The large genital shield is wedge-shaped, its posterior margin being slightly convex. The genital setae and pores lie off the shield. The post-epigynial shields are four in number. The eight pairs of ventral setae are dis-



FIGS. 12–16. *Arctoseius multidentatus* sp. nov., female. Fig. 12, ventral view. Fig. 13, lateral view. Fig. 14, gnathosoma ventral. Fig. 15, tectum. Fig. 16, chelicera.

tributed as in the figure. The metapodals are elongate. The anal shield is irregular in contour. The anal setae are all approximately equal in length.

The stigma is situated ventro-laterally between coxae III and IV (Fig. 13). The peritreme is reduced and extends as far as the middle of coxa II. The peritrematal plate is well-developed being fused into the dorsal shield anteriorly and externally around part of coxa IV posteriorly. The exopodal plates are fragmentary.

The gnathosoma has four pairs of ventral setae (Fig. 14). The corniculi are relatively long and extend beyond the anterior margin of the pedipalp trochanter by nearly half their length. The fixed digit of the chelicera is only about one and a half times as long as the corniculi. The tectum is tridentate (Fig. 15). The movable digit of the chelicera is bidentate, the fixed multidentate and with a short *pilis dentilis* (Fig. 16).

All the legs are normal for the genus.

DIMENSIONS. Length 605μ, breadth 275μ.

LOCALITY. A single female (the holotype, 1954.3.19.7) from Point Barrow, Alaska (*Coll. A. Weber*).

MESOSTIGMATA—EPICRIINA

At present there are two conflicting views on the classification of the EPICRIINA depending on the relationship between the Epicriidae and Zerconidae. Vitzthum (1941) considers these families to be closely related and includes both in the EPICRIINA, which he defines as follows :

" Gnathosoma von oben meist nicht sichtbar. Männliche Genitalöffnung inmitten des Sternale. Rumpf meist etwas flachgedrückt, so dass Rückenfläche und Bauchfläche durch eine mehr oder weniger scharfe Kante geschieden sind. Männliche Cheliceren ohne Spermatophorenträger. Weibliche Genitalöffnung ein Querspalt vor einem Genitiventrale, das zwei oder mehr Haarepaare trägt.—Bisher ist nur bei *Triangulozercon* ein dem der *Gamasides* gleichendes Herz nachgewiesen."

Trågårdh, on the other hand, disagrees with Vitzthum and in his important work on the classification of the Mesostigmata, based primarily on the structure of the sterniti-genital region in the female, places the Zerconidae in a distinct division, or cohort, the ZERCONINA. In Trågårdh (1938) the Epicriidae are included in the Sejidae (= Liroaspidae) a family of the SEJINA (= LIROASPINA) on the basis of the females possessing a primitive genital shield. This relationship between the Epicriids and Liroaspids was retained by Trågårdh (1946*a*) in a revised classification of the Mesostigmata, but later (Trågårdh, 1946*b*) the Epicriidae were removed from the LIROASPINA because of the differences in structure of the genital region of the male. This resulted in the EPICRIINA being grouped with the ZERCONINA since both had the male " aperture closed by a biarticulated plate attached at the anterior margin."

Trågårdh's separation of the EPICRIINA and ZERCONINA appears therefore to be based on a difference in the structure of the sterniti-genital region of the females, which he considered to be fundamental. Recently the writer has compared the structure of the genital plate in a number of species of *Epicrius* s. lat. and *Zercon*. In both genera the function of the plate is basically the same as in the Laelaptoidea, the only difference being in the reduction of the hyaline epigynial portion of the plate which is so well-developed in the free-living Laelaptoidea and Macrocheloidea. In *Epicrius* and *Zercon* the epigynial portion of the plate is reduced to a narrow chitinized rim so that the egg is not extruded along a " chute " as in the Laelaptoidea. Further, the males of both *Epicrius* and *Zercon* agree in a number of characters, for example, in the position of the genital orifice, in the presence of a pair of hairs on the anterior plate covering the genital orifice, and in the absence of a spermatophoral process on the chelicerae. In view of the apparent close relationship between the families the writer follows Vitzthum's concept of the EPICRIINA and proposes the following classification : Division EPICRIINA : Mites with the epigynial portion of the genital plate in the female reduced to a narrow chitinised rim overlapping the genital orifice. Male genital opening situated in the sternal shield in the region of coxae II and III and closed by two plates, the anterior of which bears a pair of hairs. Chelicerae dentate in both sexes, but without spermatophoral process in the male. Pedipalps with five free segments, specialized seta on palptarsus two or three pronged.

The EPICRIINA may be divided into the following superfamilies based on the ornamentation of the dorsal shield and the structure of the stigmata :

1. Peritreme and peritrematal plate absent in both sexes ; the stigmata enclosed in a dorsal shield richly provided with small elevations forming a polygonal network. Jugular plates well-developed in both sexes superfam. *Epicrioidea* nov.
–. Peritreme and peritrematal plates present, dorsal shield without characteristic ornamentation. Jugular plates absent in the female superfam. *Zerconoidea* nov.

The Epicrioidea contains one family only, the Epicriidae, represented by the genera *Epicrius* (with the subgenus *Diepicrius* Berl.) and *Berlesiana* Turk. The Zerconoidea contains the following families :

1. Dorsal plate divided into a notocephale and notogaster of approximately equal size. Body triangular in outline with serrated lateral margins. All legs with claws. Peritreme reduced in length. Female genital plate with a pair of setae. Specialized seta on palptarsus two-pronged fam. *Zerconidae* Berl.
–. Dorsal plate entire. Peritreme normal. Leg I in both sexes without claws. Strong sexual dimorphism in the structure of the dorsal shield. Female genital plate without setae. Specialized seta on palptarsus three-pronged fam. *Arctacaridae* nov.

The family *Zerconidae* comprises three genera, *Zercon* Koch (syn. *Triangulozercon* Jacot), *Parazercon* Trägårdh (syn. *Trizerconoides* Jacot) and *Prozecon* Sellnick. The family *Arctacaridae* is erected for *Arctacarus rostratus* gen. nov. et sp. nov. described below.

The genus *Seiodes* Berl. 1887 (genotype *Seiodes ursinus* Berl. 1887) also belongs to the Epicriina, but whether it is referable to either of the two superfamilies here diagnosed is uncertain pending a re-examination of the types. The genotype species, *S. ursinus*, has the following characters : Dorsal shield entire, ventri-anal shield occupying the greater part of the region posterior to coxae IV in both sexes. All legs with well-developed claws. Femur II in the male spurred. Male genital orifice in sternal shield between coxae III. Chelicerae of the male without a spermatophoral process. The species named *S. hystricinus* by Berlese (1892) may not be congeneric with *ursinus*.

The collection from Alaska contained two species belonging to the EPICRIINA and these are described below.

Family ZERCONIDAE

The only representative of this family is a female of the genus *Zercon*. To date four species of the genus have been recorded from the Arctic, namely, *Zercon curiosus* Trägårdh, 1910, *Zercon arctuatus* Trägårdh, 1931, *Zercon triangularis* Koch, 1836, and *Zercon solenites* Haarløv, 1942. *Z. curiosus* is recorded from a number of localities in Swedish Lappland, *Z. arctuatus* was first collected in an old orchard at Thorshavn in the Faroes (Trägårdh, 1931) and has recently been recorded from S. England by Evans (1953), *Z. triangularis*, reported from a number of localities in Spitzbergen by Thor (1930), is a widely distributed species in Europe. These three species are described and keyed in Sellnick (1944). The fourth species, *Z. solenites*, is known only from the type locality in Northern Greenland (Haarløv, 1942) and differs from the other known species of *Zercon* in having a well-developed peritreme reaching to coxa I.

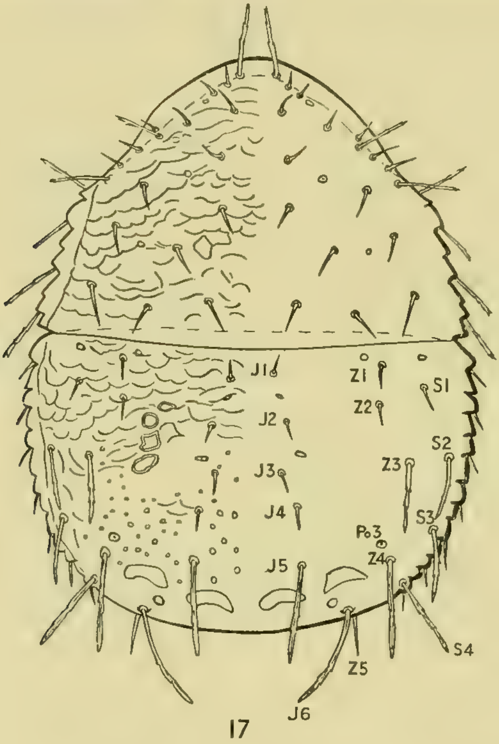
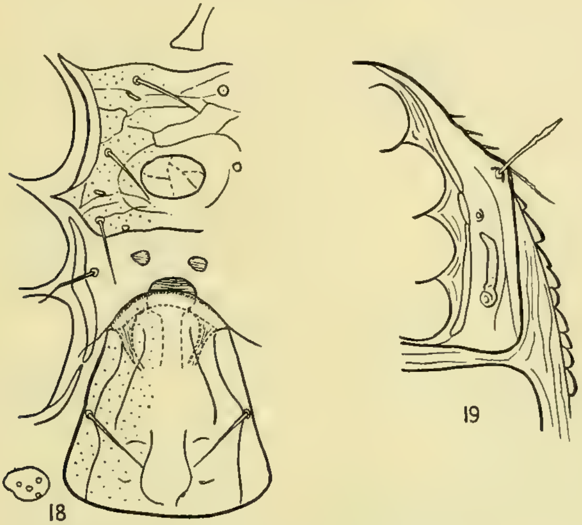


FIG. 17. *Zercon fenestralis* sp. nov., female. Fig. 17, dorsal view.

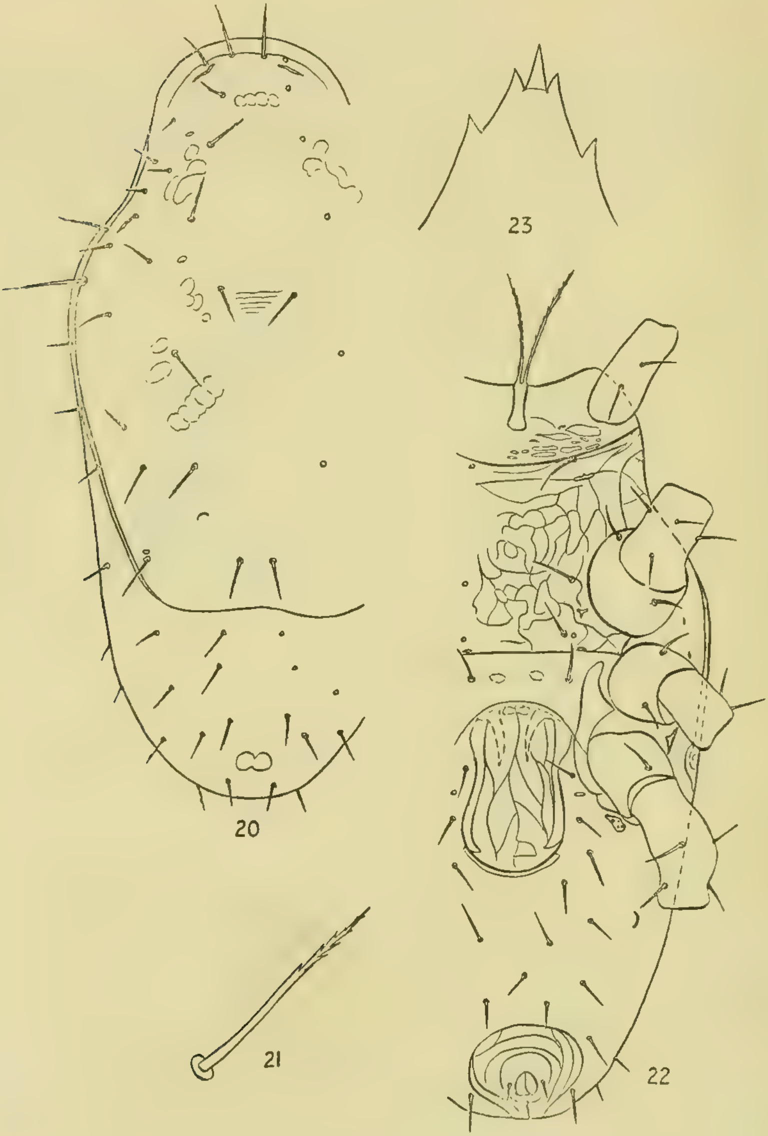
The species collected in Alaska appears to be new to science on the basis of the chaetotaxy of the dorsal shields. The nomenclature for the chaetotaxy of the notogaster follows that of Sellnick (1944).

Zercon fenestralis sp. nov.

FEMALE. The dorsum is entirely covered by two shields of approximately equal size. The anterior shield, the notocephale, bears 15 pairs of simple dorsal setae distributed as in Fig. 17. The remainder of the chaetotaxy comprises stout coarsely serrated setae. These number six pairs, including the verticals. The lateral margins of the notocephalic shield are serrated. Its surface is strongly reticulated and is provided with pores. The notogaster bears fifteen pairs of setae excluding a lateral series of seven. All the lateral setae are simple. Setae of the J series are well-developed. J1–J4 are short, simple, and of about equal length. The stout serrated setae, J5 and J6, are more than three times the length of J1–J4. Series Z comprises six setae of which Z1 and Z2 are similar to J1 and J2 in size and form. Z3 and Z4, however, resemble J5 and J6 in structure. Z3 is shorter than Z4. Z5, situated in close proximity to J6, is simple. Series S consists of four setae on either side. S1 is simple and the same length as J1 and Z1. Setae S2–S4 are stout and serrated. S1 is closer to Z1 than S2, but S2, S3 and S4 are equidistant from each other. Pore 3 is situated a short distance in front of seta Z4 and inside the line connecting Z3 and Z4. The distribution of the remaining pores is shown in the



FIGS. 18–19. *Zercon fenestralis* sp. nov., female. Fig. 18, sterniti-genital region. Fig. 19, peritreme and peritrematal plate.



FIGS. 20–23. *Arctacarus rostratus* gen. et sp. nov. Fig. 20, dorsal view. Fig. 21, dorsal seta. Fig. 22, ventral view. Fig. 23, tectum.

figure. The anterior half of the notogaster is strongly reticulated and the posterior half coarsely punctured. The four posterior depressions are conspicuous.

Ventrally, the sternal shield bears three pairs of simple setae and three pairs of pores (Fig. 18). The ornamentation is strong except for an oval area in the region of sternal setae II. The endopodal plate in the region of coxae II is fused with the lateral margin of the sternal shield. The metasternal setae are situated on the interscutal membrane posterior to the sternal shield and between them lie a pair of weakly sclerotized plates. The genital shield, truncated posteriorly, has a pair of genital setae. The epigynial portion of the plate is strongly sclerotized. The head of a club-shaped vaginal sclerite (?) protrudes from under the epigynial shield. The endopodal plate in the region of coxae III and IV is interrupted opposite the middle of coxae IV. The large ventri-anal shield is of the form normally found in the genus and bears eight pairs of simple setae (excluding the paranals and the post-anal setae).

The stigma and its short peritreme are enclosed in a large peritrematal plate truncated posteriorly and fused anteriorly with the notocephalic shield. The internal margin of the peritrematal is fused with the exopodal (Fig. 19). The peritrematal plate has a stout serrated seta and a large pore.

The legs and gnathosoma are normal for the genus.

DIMENSIONS. Length 465µ, breadth 375µ.

LOCALITY. A single female, the holotype (1954.3.19.27) from Point Barrow, Alaska (*Coll. A. Weber*).

Family ARCTACARIDAE fam. nov.

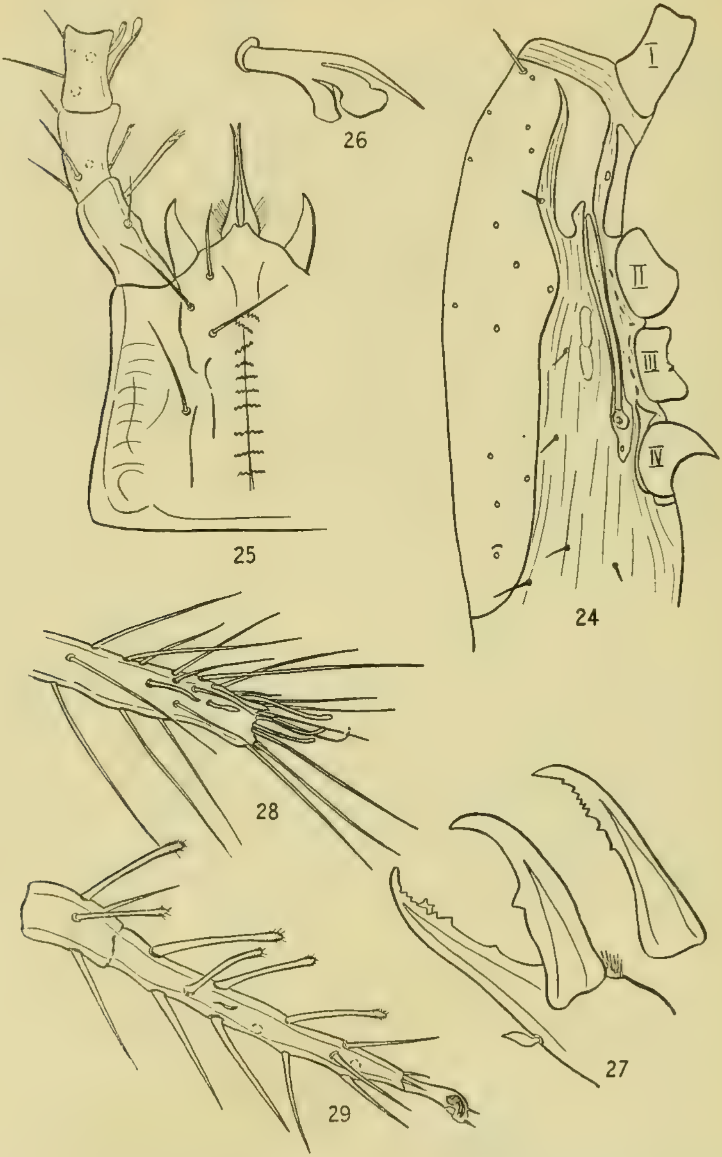
DIAGNOSIS. Dorsal shield heavily sclerotized in both sexes completely covering the dorsum of the female. Sterniti-genital region of female normal for the Epicriina. In the male the sterniti-genital plate is fragmented in the region of coxae III–IV and separated from the ventri-anal plate. Male genital orifice closed by two plates, the anterior of which is provided with a pair of stout setae. Peritrematal plate fused with the dorsal shield anteriorly in the female but fused along its entire length in the male. Coxa I, femur II and IV spurred in male. Tarsus I in both sexes without pulvillus and claws. Tarsi II–IV with pulvillus and claws. Chelicerae dentate. Specialized seta on palptarsus three-pronged.

Genus ***Arctacarus*** gen. nov.

With the characters of the family. Type : *Arctacarus rostratus* sp. nov.

Arctacarus rostratus sp. nov.

FEMALE. The dorsal shield, 820–830µ × 515–528µ, is chestnut brown in colour and does not completely cover the dorsum of the mite (Fig. 20). The surface of the shield is finely striated and the dorsal setae are setose distally (Fig. 21). The shield has a large pair of lyriform pores postero-lateral to the vertical setae and a number of smaller pores distributed as in the figure. The posterior region of the dorsum is



Figs. 24–29. *Arctacarus rostratus* gen. et. sp. nov. Fig. 24, lateral view. Fig. 25, Gnathosoma ventral. Fig. 26, specialized seta of palptarsus. Fig. 27, chelicera showing variation in the dentition of the movable digit. Fig. 28, Distal end of tarsus I. Fig. 29, tarsus IV.

not sclerotized and bears nine pairs of dorsal setae of similar form to those on the dorsal shield. Anterior to the posterior dorsal setae lies a small, weakly sclerotized plate incompletely divided into two equal-sized platelets. It is interesting to note that a pair of platelets is also present in this position in some species of *Veigaia* which have a larger dorsal shield (or shields) than *Arctacarus*.

The tritosternum is well-developed with the lacinae long and setose. The ornamented sternal shield bearing three pairs of sternal setae and three pairs of pores extends from the posterior edge of coxae I to the anterior border of coxae III (Fig. 22). It is produced into a broad sclerotized band between coxae I and II and is fused along its lateral margin with the endopodal plates. The region between the anterior margin of the sternal shield and the tritosternum is occupied by the fragmented prae-endopodal plates. The general structure of the sternal region in *Arctacarus* is not unlike that in the females of *Veigaia*. The metasternal setae lie on the interscutal membrane between the sternal shield and the anterior lip of the genital orifice. In between the metasternals lies a pair of small lightly sclerotized platelets (cf. *Zercon*). The endopodal plate in the region of coxae III and IV is well-developed and extends around the posterior border of coxae IV. The genital shield is flask-shaped, strongly ornamented and without setae ; the genital setae and pores lying lateral to the shield. The structure of the anterior (epigynial) portion of the shield is similar to that in *Zercon*. The vaginal sclerite (?), however, is not nearly as well developed. A further comparison with *Zercon* can be made in the presence of a small " pore "- bearing plate situated posterior to coxae IV. The chaetotaxy of the region between the genital and anal shields is shown in the figure. The anal shield is pear-shaped and bears three setae—the para-anals and the post-anal setae. The shield is conspicuously ornamented. The chaetotaxy of coxae I–IV, is, respectively, 2–2–2–1.

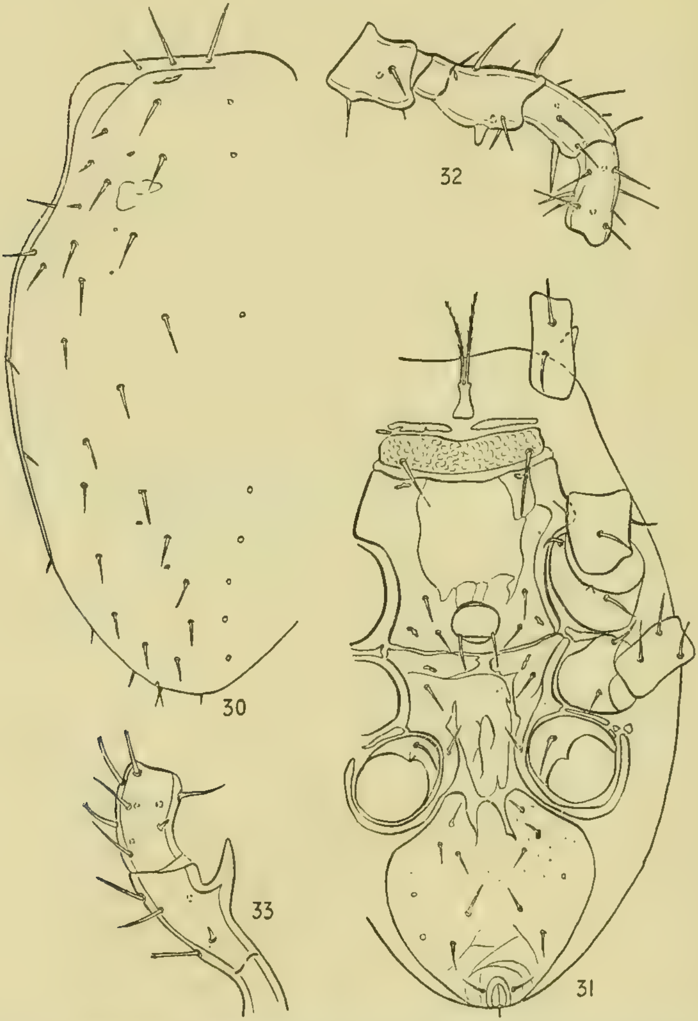
The stigma lies ventro-laterally in line with the third intercoxal space (Fig. 24). The peritreme is well-developed and extends beyond the anterior margin of coxa II. The peritrematal plate, fused at its distal end with the dorsal shield, is broad in the region of the first intercoxal space but narrows markedly lateral to coxae II–IV. It is not fused with any part of the exopodal plate. The exopodal plate in the region of coxa IV is well-developed but in the region of coxae II and III it is fragmented. The interscutal membrane between the dorsal shield and the peritrematal plate has three setae and two weakly sclerotized platelets.

Ventrally the gnathosoma bears four pairs of stout setae (Fig. 25). The external posterior rostral seta is situated midway between the anterior rostral and internal posterior rostral setae and external to the line connecting them. The floor of the ventral groove is provided with ten rows of denticles. The corniculi are pointed distally and extend a short distance beyond the middle of the palptrochanter. The chaetotaxy of the palptrochanter, femur and genu is 2–5–6. A number of the internal setae on the palpgenu, trochanter and femur are serrated distally and the two internal setae on the palp spatulate. The specialized seta on the palp tarsus is three-lobed (Fig. 26). The tectum (epistome) is large and triangular in form with five distinct projections (Fig. 23).

The dentition of the movable digit is variable. Fig. 27 shows a unidentate and multidentate form ; the latter having nine small teeth. The fixed digit has two strong teeth and five to six smaller ones. The *pilis dentilis* is of an unusual form (see figure).

Leg I, varying between 1030μ and 1045μ in length, is approximately equal in length to the body of the mite. Tarsus I is without pulvillus and claws (Fig. 28). The majority of the dorsal setae on leg IV are stout and spiculate distally (Fig. 29).

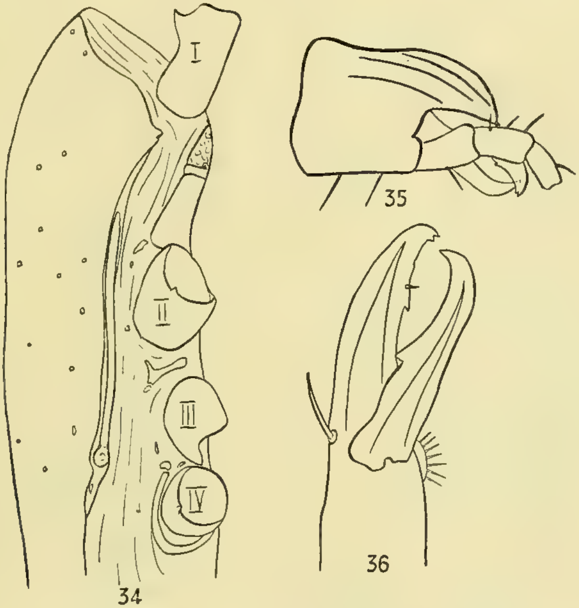
One of the females examined contained an egg measuring 400μ × 320μ.



Figs. 30–33. *Arctacarus rostratus* gen. et sp. nov., male. Fig. 30, dorsal view. Fig. 31, ventral view. Fig. 32, leg I. Fig. 33, leg IV.

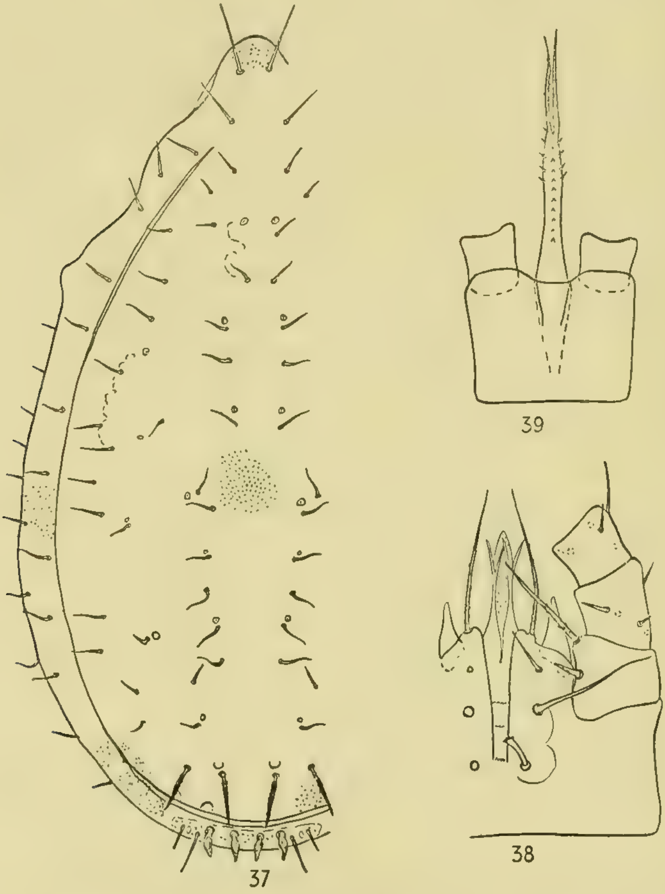
MALE. The contour of the body differs markedly from the female. The dorsal shield covers the entire dorsum of the male. The shield is broadest at the shoulders and tapers strongly towards the posterior end of the body. The chaetotactic pattern and the distribution of pores is shown in Fig. 30. The dorsal setae are serrated.

The tritosternum is basically the same as in the female (Fig. 31). The sternitigenital region is provided with a number of plates. The prae-endopodals are elongate and distinctly separate from the sternal shield. Sternal setae I are situated on the heavily ornamented anterior portion of the plate and are separated from it by a narrow strip of less strongly chitinized cuticle. Sternal setae II and III and pores I and II are placed in the weakly ornamented portion of the sternal shield extending from the middle of the first intercoxal space to the posterior margins of coxae II. The shield is not produced between coxae I and II as in the female. The genital orifice is situated in the posterior third of the shield and is closed by two plates ; the anterior of which bears two stout setae. The shield in the region between coxae II and III is fragmented and variable in form. The lateral margin of the shield is fused with the endopodal plate. In the type specimen the shield is divided longitudinally into two shields of unequal size and each shield bears two setae and the metasternal or third sternal pore. The shields are punctured. The ventri-anal shield has four pairs of pre-anal setae in addition to those setae associated with the anal region, namely, the para-anals and the post-anal setae.



FIGS. 34–36. *Arctacarus rostratus* gen. et sp. nov., male. Fig. 34, lateral view. Fig. 35, tectum. Fig. 36, chelicera.

The peritrematal plate is fused along its entire length with the lateral margin of the dorsal shield (Fig. 34). The stigma is situated laterally in the region of the third intercoxal space. The peritreme is strong and extends beyond the anterior margin of coxa II. The exopodal plate of coxa IV is well-developed and entire. The remainder of the exopodal plate is fragmented.



Figs. 37–39. *Dinychus micropunctatus* sp. nov., female. Fig. 37, dorsal view. Fig. 38, gnathosoma ventral. Fig. 39, tectum.

The gnathosome and palps are the same as in the female. The epistome (tectum) on the other hand is considerably more strongly developed than in the female and is beak-like in form (Fig. 35).

The fixed digit is bidentate and bears a short spine-like *pilus dentilis* (Fig. 36). The movable digit, without spermatophoral process, is unidentate.

Leg I is long and slender as in the female and is without pulvillus and claws. Coxa I is provided with a strong spur (Fig. 31). Legs II–IV terminate in a pulvillus and two claws. The femur of legs II and IV are spurred (Figs. 32 and 33).

DIMENSIONS. Female: Length 1050–1080µ, breadth 515–528µ. Male: Length 925–940µ, breadth 575–590µ.

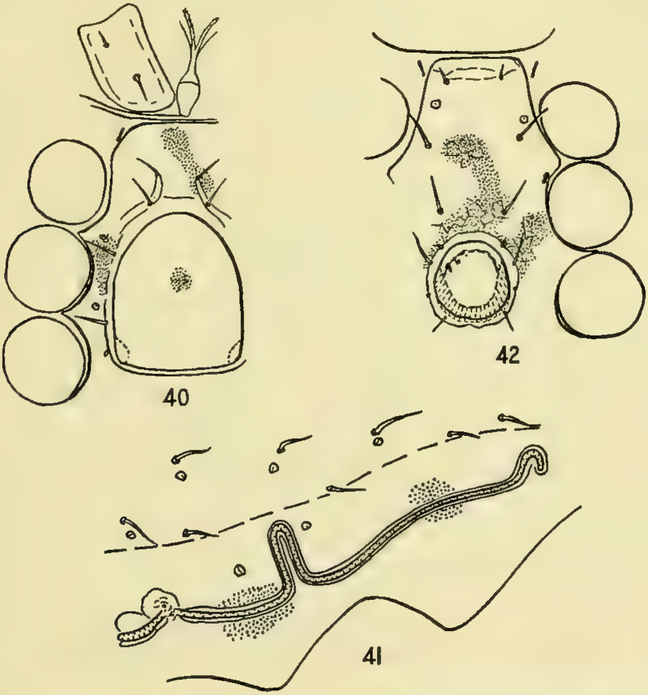
LOCALITY. Two females and four males from Point Barrow, Alaska (Coll. *A. Weber*, 1950). Holotype female (1954.3.19.21), Allotype male (1954.3.19.23) and paratypes (1954.3.19.22, 24–26).

MESOSTIGMATA—UROPODINA

Family PRODINYCHIDAE

Dinychus micropunctatus sp. nov.

FEMALE. The dorsal shield is oval in contour and densely covered with minute punctations. The chaetotaxy and distribution of pores is shown in Fig. 37. The vertex is short with the vertical setae long and stout. The two pairs of long setae situated posteriorly on the dorsal shield are setose. The marginal shield is of the



FIGS. 40–42. *Dinychus micropunctatus* sp. nov. Fig. 40, sterniti-genital region of female. Fig. 41, lateral view of female showing peritreme. Fig. 42, sterniti-genital region of male.

same structure as the dorsal shield. The posterior marginal shield bears two pairs of short, stout serrated setae and two pairs of simple setae. The latter lie on either side of the serrated setae.

The tritosternum is short and of the form shown in Fig. 40. The sternal region is covered with minute punctuations and a faint polygonal network. The anterior margin of the sternal shield is straight. Sternal setae I and II are situated between coxae II; on setae I and II on either side are place on a sclerotised ridge (Fig. 40). Sternal setae III and IV (according to Trågårdh, 1943, seta IV is the pseudosternal) lie lateral to the large epigynial shield which extends from the middle of coxae IV to the posterior margin of coxae II. The ornamentation of the epigynial shield is similar to that of the sternal shield. Four pairs of pores are present in the sterniti-genital region. The remainder of the venter of the female is typical for the genus.

The peritreme is long and convoluted. The stigma is situated ventro-lateral of coxa III (Fig. 41). The peritreme continues a short distance posterior to the stigma. Anterior to the stigma the peritreme is looped in the region of coxae II. A pore is present anterior and posterior to the loop.

The four pairs of ventral setae are distributed as in Fig. 38. The capitular setae are short and setose distally. The external posterior rostrals are long and smooth and the internal posterior rostrals, situated anterior to the exterior posterior rostrals, short and simple. The anterior rostrals are long, about equal in length to the exterior rostrals, and setose. The corniculi are short and extend to the anterior margin of the palpfemur. The chaetotaxy of the palptrochanter, femur and genu is 2–5–5). The setae on the trochanter are stout and setose. The tectum (epistome) is produced into a long, narrow process, bifid distally (Fig. 39). The shaft is covered with small spines.

All legs terminate in a pulvillus and two claws and are normal for the genus.

MALE. The structure of the dorsal shield and peritreme is similar to that of the female. The sterniti-genital region is well differentiated (Fig. 42). The genital orifice is situated between coxae IV. The distribution of setae and pores is shown in the figure. The complete venter of the male is finely punctated.

DIMENSIONS. Female: Length 670–693μ, breadth 370–375μ. Male: Length 682–715μ, breadth 380–385 μ

LOCALITY. Two females and four males from Point Barrow, Alaska (*Coll. Weber.*). Holotype female (1954.3.19.1), Allotype male (1954.3.19.2) and paratypes (1954 3.19.3–6).

Dinychus micropunctatus sp. nov. is closely related to *Dinychus sublaevis* (Trågårdh) 1943, in the chaetotaxy of the posterior dorsal region of both sexes. It differs from *D. sublaevis* in the ornamentation of the dorsal and ventral shields, and the structure of the sternal region of the female.

SUMMARY

1. A small collection of Mesostigmatid mites from Alaska comprises the following seven species:

Haemogamasus alaska Ewing.
Arctoseius ornatus sp. nov.

Arctoseius weberi sp. nov.
Arctoseius multidentatus sp. nov.
Zercon fenestralis sp. nov.
Arctacarus rostratus gen. et sp. nov.
Dinychus micropunctatus sp. nov.

2. The Arctic species (females only) of the genus *Arctoseius* Sig Thor s. str. are keyed.
3. *Tristomus* Hughes 1948 is made a synonym of *Arctoseius*.
4. The classification of the EPICRIINA is discussed and a new family ARCTACARIDAE is erected for *Arctacarus* gen. nov.

Acknowledgments

I am grateful to Dr. Max Sellnick, Stockholm, for comparing specimens of *Dinychus micropunctatus* with the type of *Dinychus sublaevis* and to Dr. H. W. Parker for his criticisms of the manuscript.

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PRESENTED

THE OTARIID SEALS OF THE PACIFIC COAST OF AMERICA

JUDITH E. KING

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ZOOLOGY Vol. 2 No. 10
LONDON : 1954

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BY

JUDITH E. KING

Pp. 309–337 *; Pls.* 10–11 ; 3 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

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THE OTARIID SEALS OF THE PACIFIC COAST OF AMERICA

By JUDITH E. KING

FROM Alaska to Cape Horn along the Pacific coast of the Americas several species of Otariid seals have been recognized. These include both fur seals and hair seals which have been exploited by commercial sealers for over two centuries; but in spite of this there has always been some doubt about the exact identities of some of the animals concerned.

SPECIFIC IDENTITY OF *ARCTOCEPHALUS GALAPAGOENSIS* HELLER

1. *Heller's type specimen*

During 1898–99 the Hopkins Stanford Galapagos Expedition collected some seal skulls from Wenman Island in the Galapagos group. The skull of an adult male animal was described by Heller (1904) as the type of *Arctocephalus galapagoensis*. This skull is now in Stanford University, California, and although Heller gave its number as 2480, Mayer (1949) gives the correct number as 2812.

Measurements of two other skulls are given by Heller: No. 2481, male, nearly adult; occipital crests low; sutures indistinct. No. 2482, female, same as 2481 in age. Mayer (1949) gives the correct numbers of these as 4442 and 4446 respectively.

The specific characters of the skull are given by Heller as, " Distinguishable from its nearest ally *A. philippi* of Juan Fernandez by its wider skull, both the zygomatic and mastoid measurements being considerably greater, and by its longer snout and mandible."

Heller gives no indication of having compared this skull with that of any other seal except *A. philippi*. Photographs of the type skull of *A. galapagoensis* (Pls. 10A and C; 11A) have been compared with skulls of *A. philippi* and *A. australis*, the two members of the genus *Arctocephalus* known to occur along the western coast of America. As Heller has stated, the skull of *A. galapagoensis* is markedly different from that of *A. philippi* but it differs not only in the characters he mentions but also in having a wider and less excavated palate, deep zygomatic arches and short broad nasals. These are just the characters in which skulls of *A. australis* differ so markedly from those of *A. philippi* and a comparison of the photographs of the skull of *A. galapagoensis* with skulls of *A. australis* shows a remarkable similarity (Pls. 10 and 11).

It should perhaps be mentioned that Heller does not indicate whether the total length of the animal from which the type skull was derived was taken from the tip of the snout to the tip of the tail or to the end of the longest digit of the hind flippers. An indication that the measurement was to the latter point is gained from dimensions which Turner (1888, *Rep. Sci. Res. H.M.S. "Challenger" Zool.* 26 : 39) gives of a specimen of an adult male *A. australis*. *They are as follows* :

From snout to tip of longest digit of pes : 5 ft. $10\frac{1}{2}$ in. (1,790 mm.).
From snout to tip of tail in straight line : 4 ft. 11 in. (1,498·6 mm.).
Extreme condylo-premaxillary length of skull : 233 mm.

The greatest length of the type skull is 214 mm. and the total length of the animal is given by Heller as 1,675 mm. (5 ft. 6 in.). Thus by comparison with Turner's measurements, the *A. galapagoensis* type skull length is in proportion to body length if the latter is taken to the end of the hind flippers and not otherwise.

Measurements and proportions of the three Galapagos skulls have been compared with those of all the *A. australis* skulls in the British Museum collection (Table I). This includes 67 skulls from the Falkland Islands, four from the Straits of Magellan, one from Lobos Island, Uruguay, two from Messier Channel, Chile, and one from Tierra del Fuego. Graphs of the measurements of the various components of the skulls expressed as percentages of their condylo-basal lengths gave no indication of allometric growth. Length ratios plotted against the condylo-basal length showed no geographical differentiation, but width ratios showed that there was some difference between the skulls from the Falkland Islands and those from the "mainland" population, including the Galapagos Islands. Taking the zygomatic width as an example and using a graphical method the zygomatic width expressed as a percentage of the condylo-basal length in the Falkland sample has a mean value of 57·2%, a standard deviation of 2·5, and a standard error of the mean of 0·29. The corresponding figures for the mainland sample including those from the Galapagos, are 61, 3·2, and 0·96. The difference between these means is 3·8 and the standard error of the difference of the means is 1. The ratio $\frac{d}{\sigma d}$ is therefore 3·8. A difference of this magnitude would occur twice in 10,000 trials, but only once in 10,000 in the direction observed. This is statistically significant and indicates that the *A. australis* population on the Falkland Islands is slightly different from that inhabiting the South American coast and adjacent islands, but there are not enough skulls in the collection to see whether the individual mainland populations are in any way distinct from one another. The zygomatic width proportions of the Galapagos skulls are within the standard deviation of the mainland sample and slightly above that of the Falkland Islands sample.

TABLE I.—*Measurements and proportions of skulls of* A. australis
(See notes on measurements used)
FALKLAND ISLANDS

Registered No. and sex, if known	1949.3.17.1 Male		1949.3.17.2		1949.3.17.3		1949.3.17.4	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	248		247		248		243	
Condylo-basal length	241	100	239	100	246	100	239	100
Zygomatic breadth	155	64·3	143	59·8	138	56·1	146	61·1
Snout length	73	30·3	73	30·5	75	30·5	70	29·3
Snout width at canines	52	21·6	57	23·8	58	23·6	54	22·6
Snout width at level of 2nd cheek tooth	48	19·9	46	19·2	45	18·3	46	19·2
Anterior breadth nasals	34	14·1	32	13·4	35	14·2	29	12·1
Greatest length nasals	36	14·9	41	17·2	36	14·6	38	15·9
Least interorbital width*	32	13·3	35	14·6	29	11·8	29	12·1
Mastoid breadth	142	58·9	134	56·1	126	51·2	129	53·9
Length upper tooth-row i.—m. 6	92	38·2	88	36·8	96	39·0	89	37·2

Registered No. and sex, if known	1949.3.17.5		1949.3.17.6 Male		1949.3.17.7		1949.3.17.8	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	239		249		237		248	
Condylo-basal length	235	100	242	100	233	100	244	100
Zygomatic breadth	132	56·2	140	57·9	138	59·2	145	59·4
Snout length	73	31·1	73	30·2	72	30·9	74	30·3
Snout width at canines	54	22·1	54	22·3	55	23·6	59	24·2
Snout width at level of 2nd cheek tooth	45	19·1	45	18·6	46	19·7	51	20·9
Anterior breadth nasals	30	12·8	32	13·2	34	14·6	32	13·1
Greatest length nasals	32	13·6	35	14·5	40	17·2	40	16·4
Least interorbital width*	25	10·6	28	11·6	29	12·4	29	11·9
Mastoid breadth	126	53·6	137	56·6	129	55·4	134	54·9
Length upper tooth-row i.—m. 6	88	37·4	92	38·0	92	39·5	92	37·7

Registered No. and sex, if known	1949.3.17.9		1949.3.17.10		1949.3.17.11		1949.3.17.12	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	240		239		239		255	
Condylo-basal length	233	100	234	100	233	100	247	100
Zygomatic breadth	138	59·2	139	59·4	128	54·9	146	59·1
Snout length	72	30·9	70	29·9	68	29·2	76	30·8
Snout width at canines	50	21·5	48	20·5	51	21·9	57	23·1
Snout width at level of 2nd cheek tooth	41	17·6	41	17·5	44	18·9	49	19·8
Anterior breadth nasals	29	12·4	30	12·8	30	12·9	34	13·8
Greatest length nasals	38	16·3	38	16·2	35	15·0	38	15·4
Least interorbital width*	31	13·3	27	11·5	30	12·9	28	11·3
Mastoid breadth	129	55·4	126	53·8	128	54·9	137	55·5
Length upper tooth-row i.—m. 6	82	35·2	88	37·6	87	37·3	95	38·5

* Posterior to supraorbital processes.

FALKLAND ISLANDS—*continued*

Registered No. and sex, if known	1949.3.17.13		1949.3.17.14		1949.3.17.15		1949.3.17.17	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	232		239		231		235	
Condylo-basal length	225	100	233	100	225	100	226	100
Zygomatic breadth	134	59·6	135	57·9	144	64·0	124	54·9
Snout length	67	29·8	70	30·0	68	30·2	70	30·9
Snout width at canines	46	20·4	50	21·5	52	23·1	49	21·7
Snout width at level of 2nd cheek tooth	40	17·8	42	18·0	44	19·6	42	18·6
Anterior breadth nasals	28	12·4	29	12·4	31	13·8	28	12·4
Greatest length nasals	36	16·0	33	14·2	35	15·6	34	15·0
Least interorbital width*	30	13·3	30	12·9	29	12·9	25	11·1
Mastoid breadth	123	54·7	126	54·1	132	58·7	115	50·9
Length upper tooth-row i.—m. 6	85	37·8	87	37·3	88	39·1	88	38·9

Registered No. and sex, if known	1949.3.17.18		1949.3.17.19		1949.3.17.20		1949.3.17.21 Male	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	233		228		224		225	
Condylo-basal length	227	100	223	100	219	100	220	100
Zygomatic breadth	123	54·2	128	57·4	124	56·6	134	60·9
Snout length	67	29·5	65	29·1	64	29·2	66	30·0
Snout width at canines	46	20·3	50	22·4	45	20·5	50	22·7
Snout width at level of 2nd cheek tooth	37	16·3	41	18·4	38	17·4	42	19·1
Anterior breadth nasals	26	11·5	29	13·0	—	—	32	14·5
Greatest length nasals	35	15·4	33	14·8	—	—	33	15·0
Least interorbital width*	30	13·2	29	13·0	32	14·6	29	13·2
Mastoid breadth	113	49·8	121	54·3	114	52·1	125	56·8
Length upper tooth-row i.—m. 6	87	38·3	86	38·6	86	39·3	84	38·2

Registered No. and sex, if known	1949.3.17.22		1949.3.17.23		1949.3.17.24		1949.3.17.25	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	228		220		220		217	
Condylo-basal length	222	100	216	100	214	100	211	100
Zygomatic breadth	131	59·0	128	59·3	124	57·9	117	55·5
Snout length	69	31·1	64	29·6	65	30·4	60	28·4
Snout width at canines	47	21·2	44	20·4	46	21·5	42	19·9
Snout width at level of 2nd cheek tooth	42	18·9	36	16·7	39	18·2	37	17·5
Anterior breadth nasals	30	13·5	28	12·9	26	12·1	27	12·8
Greatest length nasals	36	16·2	36	16·7	33	15·4	37	17·5
Least interorbital width*	31	13·9	33	15·3	33	15·4	32	15·2
Mastoid breadth	117	52·7	115	53·2	117	54·7	108	51·2
Length upper tooth-row i.—m. 6	88	39·6	83	38·4	82	38·3	81	38·4

* Posterior to supraorbital processes.

FALKLAND ISLANDS—*continued*

Registered No. and sex, if known	1949.3.17.26		1949.3.17.27		1949.3.17.28		1949.3.17.29	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	213		214		215		219	
Condylo-basal length	209	100	210	100	210	100	214	100
Zygomatic breadth	118	56·5	117	55·7	114	54·3	127	59·3
Snout length	61	29·2	59	28·1	61	29·0	63	29·4
Snout width at canines	43	20·6	44	20·9	42	20·0	48	22·4
Snout width at level of 2nd cheek tooth	36	17·2	37	17·6	34	16·2	39	18·2
Anterior breadth nasals	27	12·9	28	13·3	24	11·4	29	13·6
Greatest length nasals	31	14·8	31	14·8	31	14·8	31	14·5
Least interorbital width*	31	14·8	28	13·3	27	12·9	34	15·9
Mastoid breadth	110	52·6	113	53·8	106	50·5	115	53·7
Length upper tooth-row i—m. 6	80	38·3	83	39·5	80	38·1	81	37·9

Registered No. and sex, if known	1949.3.17.30		1949.3.17.31		1949.3.17.32 Male		1949.3.17.33	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	222		218		214		215	
Condylo-basal length	218	100	212	100	212	100	209	100
Zygomatic breadth	122	55·9	115	54·2	116	54·7	115	55·0
Snout length	66	30·3	63	29·7	59	27·8	59	28·2
Snout width at canines	47	21·6	42	19·8	39	18·4	40	19·1
Snout width at level of 2nd cheek tooth	41	18·8	37	17·5	35	16·5	35	16·7
Anterior breadth nasals	29	13·3	28	13·2	26	12·3	24	11·5
Greatest length nasals	31	14·2	30	14·2	28	13·2	31	14·8
Least interorbital width*	29	13·3	35	16·5	26	12·3	29	13·9
Mastoid breadth	108	49·5	102	48·1	102	48·1	102	48·8
Length upper tooth-row i.—m. 6	85	38·9	84	39·6	83	39·2	—	—

Registered No. and sex, if known	1949.3.17.34		1949.3.17.35 Male		1949.3.17.36		1949.3.17.37 Male	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	213		205		197		197	
Condylo-basal length	209	100	203	100	191	100	193	100
Zygomatic breadth	119	56·9	108	53·2	104	54·5	107	55·4
Snout length	61	29·2	59	29·1	54	28·3	51	26·4
Snout width at canines	43	20·6	38	18·7	37	19·4	36	18·7
Snout width at level of 2nd cheek tooth	37	17·7	34	16·7	33	17·3	33	17·1
Anterior breadth nasals	25	11·9	24	11·8	23	12·0	23	11·9
Greatest length nasals	32	15·3	31	15·3	28	14·7	29	15·0
Least interorbital width*	27	12·9	30	14·8	31	16·2	35	18·1
Mastoid breadth	107	51·2	101	49·8	91	47·6	96	49·7
Length upper tooth-row i.—m. 6	81	38·8	78	38·4	76	39·8	71	36·8

* Posterior to supraorbital processes.

FALKLAND ISLANDS—*continued*

Registered No. and sex, if known	1949.3.17.38		1949.3.17.39		1949.3.17.40 Male		1949.3.17.41	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	184		190		187		180	
Condylo-basal length	181	100	187	100	184	100	177	100
Zygomatic breadth	98	54·1	102	54·5	100	54·3	101	57·1
Snout length	50	27·6	49	26·2	50	27·2	48	27·1
Snout width at canines	36	19·9	31	16·6	34	18·5	33	18·6
Snout width at level of 2nd cheek tooth	31	17·1	27	14·4	30	16·3	29	16·4
Anterior breadth nasals	23	12·7	22	11·8	23	12·5	22	12·4
Greatest length nasals	26	14·4	31	16·6	28	15·2	27	15·3
Least interorbital width*	34	18·8	28	14·9	35	19·0	37	20·9
Mastoid breadth	86	47·5	93	49·7	88	47·8	86	48·6
Length upper tooth-row i.—m. 6	71	39·2	70	37·4	72	39·1	70	39·5

Registered No. and sex, if known	1949.3.17.42 Male		1949.3.17.44		1949.4.17.46		1949.3.17.51	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	229		243		245		222	
Condylo-basal length	225	100	236	100	239	100	217	100
Zygomatic breadth	124	55·1	140	59·3	141	58·9	121	55·8
Snout length	65	28·9	71	30·1	72	30·1	63	29·0
Snout width at canines	46	20·4	52	22·0	51	21·3	44	20·3
Snout width at level of 2nd cheek tooth	38	16·9	44	18·6	45	18·8	38	17·5
Anterior breadth nasals	28	12·4	33	13·9	35	14·6	27	12·4
Greatest length nasals	34	15·1	36	15·3	38	15·9	34	15·7
Least interorbital width*	24	10·7	23	9·7	30	12·6	26	11·9
Mastoid breadth	116	51·6	126	53·4	136	56·9	109	50·2
Length upper tooth-row i.—m. 6	87	38·7	86	36·4	91	38·1	84	38·7

Registered No. and sex, if known	1949.3.17.53		1949.3.17.57		1949.3.17.58		1949.3.17.59	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	192		175		223		169	
Condylo-basal length	188	100	172	100	220	100	167	100
Zygomatic breadth	104	55·3	102	59·3	118	53·6	96	57·5
Snout length	54	28·7	49	28·5	65	29·5	45	26·9
Snout width at canines	36	19·1	37	21·5	42	19·1	29	17·4
Snout width at level of 2nd cheek tooth	34	18·1	31	18·0	36	16·4	28	16·8
Anterior breadth nasals	24	12·8	—	—	30	13·6	22	13·2
Greatest length nasals	28	14·9	27	15·7	32	14·5	25	14·9
Least interorbital width*	35	18·6	35	20·3	32	14·5	—	—
Mastoid breadth	94	50·0	87	50·6	112	50·9	84	50·3
Length upper tooth-row i.—m. 6	73	38·8	66	38·4	89	40·5	66	39·5

* Posterior to supraorbital processes.

FALKLAND ISLANDS—*continued*

Registered No. and sex, if known	1949.3.17.60		1949.3.17.62		1949.3.17.63		1949.3.17.64	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	208		220		213		167	
Condylo-basal length	204	100	216	100	209	100	164	100
Zygomatic breadth	114	55·9	123	56·9	120	57·4	94	57·3
Snout length	56	27·5	65	30·1	60	28·7	43	26·2
Snout width at canines	40	19·6	46	21·3	45	21·5	29	17·7
Snout width at level of 2nd cheek tooth	34	16·7	39	18·1	40	19·1	27	16·5
Anterior breadth nasals	25	12·3	28	12·9	27	12·9	17	10·4
Greatest length nasals	27	13·2	36	16·7	33	15·8	24	14·6
Least interorbital width*	34	16·7	33	15·3	36	17·2	32	19·5
Mastoid breadth	102	50·0	112	51·9	107	51·2	85	51·8
Length upper tooth-row i.—m. 6	82	40·2	86	39·8	82	39·2	64	39·2

Registered No. and sex, if known	1949.3.17.65		1949.3.17.66		1949.3.17.67		1949.3.17.68	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	231		188		180		236	
Condylo-basal length	226	100	184	100	177	100	230	100
Zygomatic breadth	119	52·7	97	52·7	101	57·1	136	59·1
Snout length	66	29·2	47	25·5	47	26·6	72	31·3
Snout width at canines	43	19·0	34	18·5	31	17·5	52	22·6
Snout width at level of 2nd cheek tooth	36	15·9	27	14·7	28	15·8	42	18·3
Anterior breadth nasals	—	—	23	12·5	—	—	—	—
Greatest length nasals	35	15·5	25	13·6	—	—	—	—
Least interorbital width*	29	12·8	37	20·1	30	16·9	28	12·2
Mastoid breadth	107	47·3	85	46·2	92	51·9	119	51·7
Length upper tooth-row i.—m. 6	89	39·4	70	38·0	66	37·3	90	39·1

Registered No. and sex, if known	1949.3.17.69		1949.3.17.71		1949.3.17.72		1949.3.17.73	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	221		210		211		214	
Condylo-basal length	215	100	206	100	206	100	213	100
Zygomatic breadth	114	53·0	117	56·8	115	55·8	119	55·9
Snout length	65	30·2	59	28·6	60	29·1	64	30·0
Snout width at canines	48	22·3	41	19·9	40	19·4	45	21·1
Snout width at level of 2nd cheek tooth	39	18·1	35	16·9	33	16·0	37	17·4
Anterior breadth nasals	24	11·2	22	10·7	26	12·6	—	—
Greatest length nasals	29	13·5	31	15·0	33	16·0	31	14·6
Least interorbital width*	25	11·6	29	14·1	28	13·6	26	12·2
Mastoid breadth	—	—	103	50·0	107	51·9	112	52·6
Length upper tooth-row i.—m. 6	83	38·6	77	37·4	77	37·4	86	40·4

* Posterior to supraorbital processes.

FALKLAND ISLANDS—*continued*

Registered No. and sex, if known	1949.3.17.75		1949.3.17.80		1949.3.17.81		1950.11.14.1 ? Male	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	216		217		197		225	
Condylo-basal length	212	100	213	100	194	100	218	100
Zygomatic breadth	115	54·2	118	55·4	109	56·2	132	60·6
Snout length	62	29·2	61	28·6	54	27·8	67	30·7
Snout width at canines	40	18·9	43	20·2	36	18·6	49	22·5
Snout width at level of 2nd cheek tooth	35	16·5	36	16·9	30	15·5	41	18·8
Anterior breadth nasals	—	—	26	12·2	25	12·9	31	14·2
Greatest length nasals	—	—	33	15·5	27	13·9	38	17·4
Least interorbital width*	38	17·9	29	13·6	27	13·9	25	11·5
Mastoid breadth	108	50·9	107	50·2	101	52·1	125	57·3
Length upper tooth-row i.—m. 6	82	38·7	85	39·9	76	39·2	81	37·2

Registered No. and sex, if known	1950.11.14.2		1855.12.26.167		1013*e*	
	mm.	%	mm.	%	mm.	%
Greatest length	219		239		143	
Condylo-basal length	213	100	235	100	141	100
Zygomatic breadth	122	57·3	145	61·7	80	56·7
Snout length	64	30·0	71	30·2	38	26·9
Snout width at canines	44	20·7	57	24·3	29	20·6
Snout width at level of 2nd cheek tooth	38	17·8	48	20·4	27	19·1
Anterior breadth nasals	28	31·1	30	12·8	18	12·8
Greatest length nasals	31	14·6	40	17·0	21	14·9
Least interorbital width*	28	13·1	32	13·6	32	24·1
Mastoid breadth	—	—	135	57·4	73	51·8
Length upper tooth-row i.—m. 6	5 teeth	—	88	37·4	57	40·4

	MESSIER CHANNEL, CHILE				STRAITS OF MAGELLAN			
Registered No. and sex, if known	1950.11.14.4 Male		1950.11.14.3 Female		1879.8.21.5 Male		1880.7.28.12	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	230		201		205		226	
Condylo-basal length	225	100	196	100	201	100	220	100
Zygomatic breadth	132	58·7	116	59·2	112	55·7	135	61·4
Snout length	66	29·3	60	30·6	56	27·9	66	30·0
Snout width at canines	55	24·4	36	18·4	35	17·4	50	22·7
Snout width at level of 2nd cheek tooth	46	20·4	35	17·9	32	15·9	41	18·6
Anterior breadth nasals	31	13·	26	13·3	22	10·9	—	—
Greatest length nasals	35	15·6	30	15·3	29	14·4	—	—
Least interorbital width*	32	14·2	26	13·3	27	13·4	—	—
Mastoid breadth	128	56·9	106	54·1	100	49·8	124	56·4
Length upper tooth-row i.—m. 6	87	38·7	80	40·8	79	39·3	85	38·6

* Posterior to supraorbital processes.

	STRAITS OF MAGELLAN—*continued*				LOBOS ISLANDS, URUGUAY		TIERRA DEL FUEGO	
Registered No. and sex, if known	1880.7.28.7		1919.7.7.10090		1947.7.16.4 Female		1880.7.28.17	
	mm.	%	mm.	%	mm.	%	mm.	%
Greatest length	226		128		210		131	
Condylo-basal length	223	100	126	100	207	100	129	100
Zygomatic breadth	146	65·5	80	63·5	131	63·3	74	57·4
Snout length	70	31·4	34	26·9	64	30·9	36	27·9
Snout width at canines	53	23·8	26	20·6	48	23·2	28	21·7
Snout width at level of 2nd cheek tooth	46	20·6	25	19·8	42	20·3	26	20·2
Anterior breadth nasals	31	13·9	17	13·5	32	15·5	17	13·2
Greatest length nasals	33	14·8	18	14·3	32	15·5	20	15·5
Least interorbital width*	34	15·2	36	28·6	31	14·9	35	27·1
Mastoid breadth	125	56·1	66	52·4	113	54·6	67	51·9
Length upper tooth-row i.—m. 6	87	39·0	62	49·2	82	39·6	54	41·9

	GALAPAGOS ISLANDS					
Registered No. and sex, if known	2812 Type male		2481 Female		2482 Female	
	mm.	%	mm.	%	mm.	%
Greatest length	214		203		200	
Condylo-basal length	211	100	200	100	197	100
Zygomatic breadth	134	63·5	124	62·0	120	60·9
Snout length	62	29·4	—	—	—	—
Snout width at canines	54	25·7	—	—	—	—
Snout width at level of 2nd cheek tooth	42	19·9	—	—	—	—
Anterior breadth nasals	27·5	13·0	22	11·0	22	11·2
Greatest length nasals	38	18·0	—	—	—	—
Least interorbital width*	25	11·8	28	14·0	27	13·7
Mastoid breadth	126	59·7	—	—	—	—
Length upper tooth-row i.—m. 6	86	40·8	80	40·0	75	38·1

* Posterior to supraorbital processes.

The length measurements show that the mainland skulls tend to be rather smaller than Falkland skulls of approximately the same age. Photographs of the Galapagos skull show that it is considerably more adult in appearance than its small size would suggest. Skulls of similar condylo-basal length from the Falkland Islands are obviously from young animals (Pl. 11). They have no sagittal crest, practically no occipital crest and the zygomatic arch has not yet attained the great depth that it does in the old animal. Heller describes the Galapagos type skull as " old adult ; sutures largely obsolete ; occipital and parietal crests high," and the photographs show these characters of age, as well as the deep zygomatic arch.

The fact that there is tending to be a smaller mainland race of *A. australis* and a larger Falkland Island race is interesting in the light of a recent paper by Sivertsen (1953) on a new species *Zalophus wollebaeki* from the Galapagos Islands. Measurements of 20 skulls of this new species were compared with those of 21 *Zalophus* skulls from California. The mean condylo-basal length of the Galapagos skulls was 264 mm., with a maximum of 276 mm., while the corresponding figures for the Californian skulls were 292 mm. and 323 mm. The type of *Z. wollebaeki*, an old male, had a condylo-basal length of 267 mm., with a high sagittal crest and very worn teeth, while the only Californian skull of a similar age had a condylo-basal length of 323 mm.

Thus while there can be no doubt that the fur seal on the Galapagos Islands is *A. australis*, the comparative measurements given here (Table I) make it seem probable that there is a race of smaller animals living on the islands. There is not at the moment sufficient material in the collection to be able to distinguish the Galapagos population from other communities living on or close to the mainland of South America, and it is for this reason that subspecific rank cannot be given to the Galapagos fur seals. The type locality for *A. australis* Zimmermann is the Falkland Islands, so that if this population is considered subspecifically distinct from that on the mainland, the name should be *A. australis australis*. Since the individual populations on the mainland cannot be separated subspecifically, the first available name for the whole is *A. australis gracilis* Nehring 1887, and should the Galapagos population eventually prove to be distinct *A. australis galapagoensis* is available. As the main purpose of the present paper does not principally concern the genus *Zalophus*, and pending the publication of Sivertsen's more comprehensive paper on the *Otariidae*, *Z. wollebaeki* may be regarded as bearing the same relation to *Z. californianus* that the Galapagos *Arctocephalus* bears to *A. australis*.

2. *Townsend's specimens*

During 1932 and 1933 several living fur seals were captured at the Galapagos Islands and sent to the San Diego Zoological Gardens. Three of these animals (an adult male, an adult female and a juvenile) died, and their skins and skulls form the subject of a paper by Townsend (1934) who referred them to *Arctocephalus galapagoensis* Heller. As Heller's desciption of the type of this species, particularly of the skull is not very detailed, and he published no photograph or drawing of the skull, Townsend seems to have based his identification mainly on the locality. He says that he compared his skulls with those of *Arctocephalus* collected " in the Straits of Magellan and on the beaches at the Galapagos and from Guadalupe," but gives no details of this comparison. A few measurements of the *Arctocephalus* from the Straits of Magellan are inserted in a list of measurements of the male skull from the Galapagos, but no reference is made to these in the text.

As the animals described by Townsend are fur seals of the genus *Arctocephalus* the photograph of the skull of one of them has been compared with those of A. *australis* and *A. philippi*, the only fur seals known to occur off the coast of South America. It is at once obvious from the general similarity, and in particular from the broad snout, wide palate, short nasals and deep zygomatics that the animals received by Townsend from the Galapagos are Southern fur seals, *Arctocephalus australis*.

Townsend gives the length of the male carcase as 4 ft. 6 in. from the tip of the nose to the tip of the tail, and the greatest basal length of the skull as 212 mm.

Townsend's measurements of the male skull are given together with those of a skull of *A. australis* (1880.7.28.7) in the British Museum collection (Table II). It is evident from the table that there is a close similarity between the two skulls. The two measurements that show most divergence are those involving interorbital width. With regard to these it may be said that the British Museum collection includes specimens of length comparable to that of Townsend's with smaller interorbital width, and the variability of this part of the skull is striking.

TABLE II.

(See notes on measurements used)

	Measurements of male skull given by Townsend		*A. australis* 1880.7.28.7	
		%		%
Greatest length	212		226	
Condylo-basal length	208*	100	223	100
Basal length (gnathion-basion)	202	97·1	214	95·9
Basilar length (basion-henselion)	198	95·2	209	93·7
Palatal length (gnathion-palation)	99	47·6	103	46·2
Zygomatic breadth	132	63·5	146	65·5
Canine to last upper molar (inclusive)	68	32·7	70	31·4
Distance between upper canines (internally)	26	12·5	25	11·2
Distance between 3rd upper molars (internally)	27	12·9	33	14·8
Interorbital width (anterior to supraorbital process)	27	12·9	40	17·9
Interorbital width (posterior to supraorbital process)	26·5	12·7	34	15·2
Width of supraorbital processes	46	22·1	58 est.	26·0
Greatest length nasals	29	13·9	33	14·8
Ant. breadth nasals	25·5	12·3	31	13·9
Breadth rostrum at 2nd molar	44	21·2	46	20·6
Mastoid breadth	117	56·3	125	56·1

* Condylo-basal length estimated as it is not given by Townsend.

SPECIFIC IDENTITY OF *ARCTOCEPHALUS TOWNSENDI* MERRIAM

The other fur seal of the genus *Arctocephalus* from the American coast, *A. philippi*, was described in 1866 by Peters from the skull of an adult (but not old) male animal collected on Juan Fernandez in December, 1864, by Dr. Philippi. Full size drawings

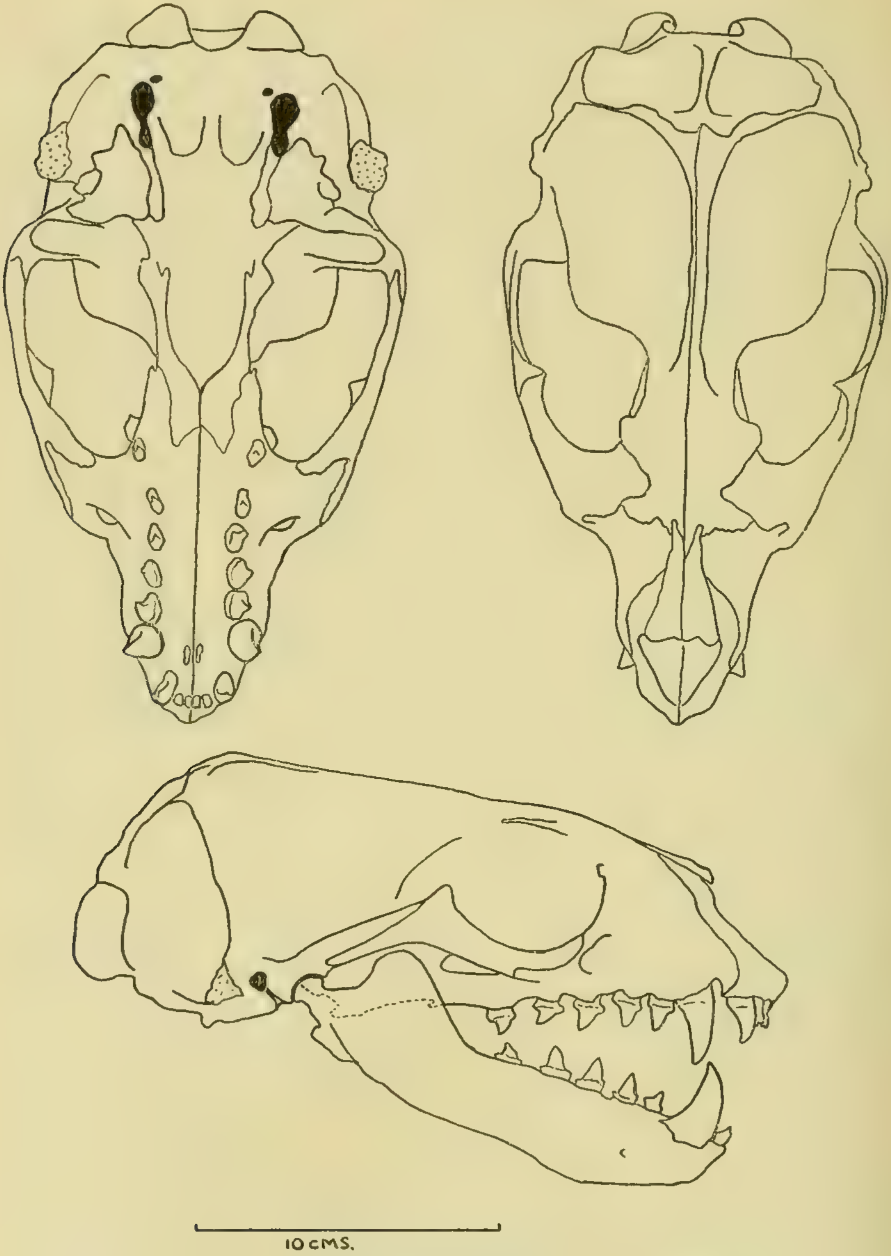

FIG. 1. Type skull of *Arctocephalus philippi* from Peters, *Monatsb. Akad. Berlin*, 1866, pl. 11.

of the skull were given (Fig. 1) from which measurements have been taken for comparison. The most important skull characters for distinguishing the species are given by Peters as follows:

1. The palate is deep in front and shallow behind, and is twice as broad between the last molars as between the canines.
2. The posterior ends of the maxillae are prolonged into small hooks.[1]
3. The maxillary root of the zygomatic arch is very broad antero-posteriorly.
4. The tympanic bullae are flat.
5. The mastoid process is long, but does not jut out ventrally.
6. The zygomatic arch is narrow.
7. The lower jaw has no pronounced angle; the coronoids are rounded and project backwards.
8. The peculiar pointed form and the lack or weak development of accessory cusps on the molar teeth, which are separated from each other by relatively large spaces.

All these characters are visible both in Peters' drawings of the type skull and in a skull of this species from Juan Fernandez in the British Museum collection (Reg. No. 1883.11.8.1.).

A. philippi, the type locality of which is Juan Fernandez, is a fur seal, as is evident from Peters' description of the long overfur and the thick underfur. The only other animal with which it may be confused is the Southern fur seal, *A. australis*, which ranges from Uruquay, round the Straits of Magellan and along the west coast of South America. Externally *A. philippi* may be distinguished from *A. australis* chiefly by its long tapering snout which is very unlike the short, rather upturned snout of *A. australis*. When seen side by side skulls of the two species show many differences. The skull of *A. philippi* (Fig. 1) is more finely built than that of *A. australis* (Fig. 2). In general shape it is long and slender, as are also the nasal bones; and the zygomatic arches are narrow in lateral view. The palate is also narrow and is very concave between molars 1–3. The skull of *A. australis* is much more robust, the nasals are short and broad, the palate is not particularly narrow or concave and the zygomatic arches are strong and deep. These differences can easily be seen in the drawings of the two skulls (Figs. 1 and 2).

In 1870 the Museum at Santiago was presented with a male, a female and a young seal from the island of Masafuera. These were considered to be a new species and formed the subject of a paper in 1871 in which they were called *Otaria argentata* (Philippi in Peters, 1871). Philippi gives a drawing of the skull of this new species and a list of characters in which it differs from *A. philippi*. The skin of *O. argentata* is said to differ chiefly by its lighter colour and by the guard hairs of the neck being shorter than those of *A. philippi*. The measurements given of the stuffed male show it to be a young animal as it is only 3 ft. 9 in. from nose to tail, and Philippi himself says that the skull is not fully grown as the crests are not developed. The length of the neck hairs and many of the characters of the skull used by Philippi to distinguish the species may be explained by the youth of the specimen, and the drawing

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[1] Not confined to this species

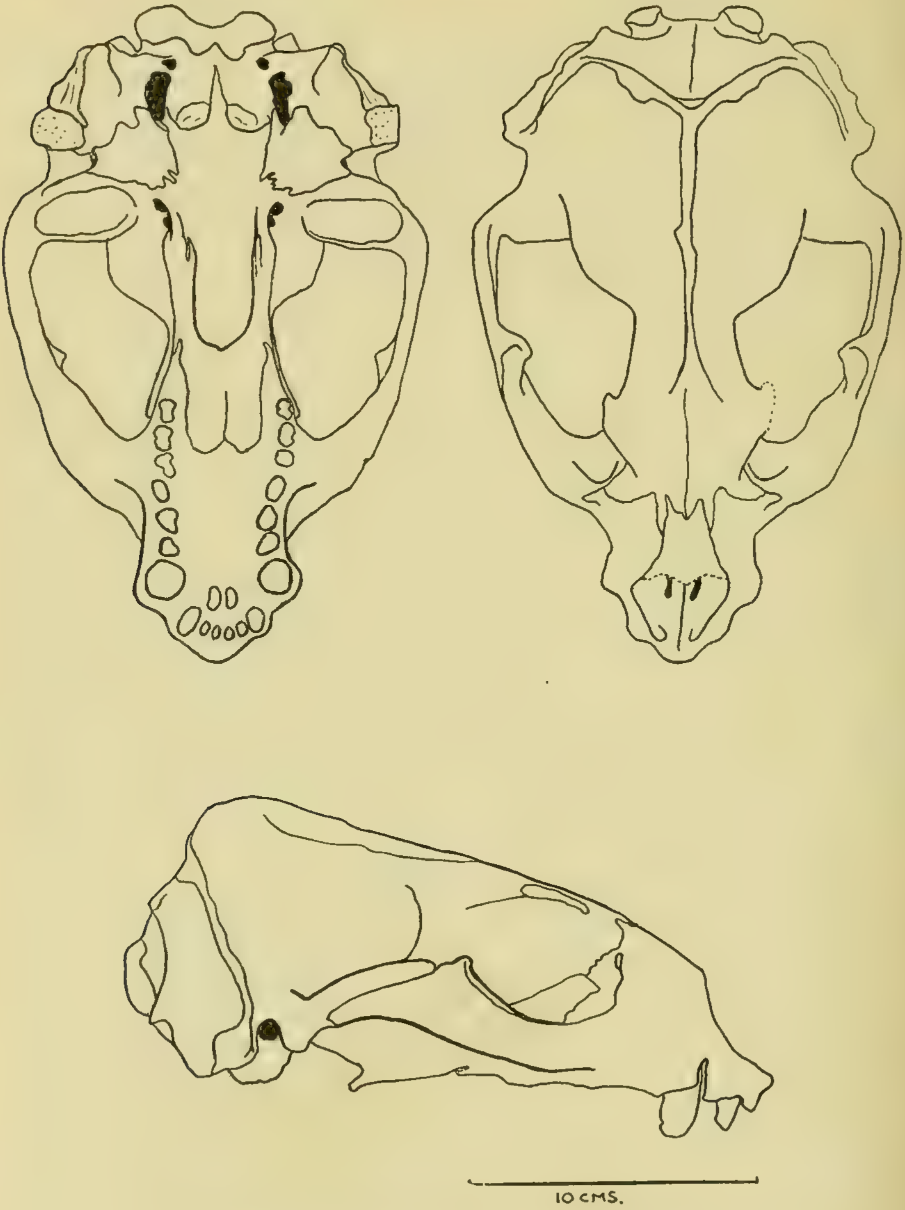


FIG. 2. Orthographic projection of skull of *Arctocephalus australis*, 1880.7.28.7.

of the skull gives proof that the animal is another specimen of *A. philippi*. Peters, in his discussion of Philippi's letter, says that if it had not been for Philippi's insistence that *O. argentata* and *A. philippi* were different, he " would have thought twice about describing them as two different species."

In 1892 an expedition sailed from San Diego to Guadalupe for the purpose of identifying the fur seals present on the island. Seven seals were seen and one was shot, but sank. Four skulls were picked up on the beach and one of these forms the type of a new species *Arctocephalus townsendi* which was described by Merriam in 1897. The skull is that of an adult male No. 83617 U. S. National Museum. Merriam compares this type " with skulls of *Arctocephalus* (*australis* or *philippi*) from the Galapagos Islands," and from the characters that he gives it is evident that he compared his skull with *A. australis* and had not seen a skull of *A. philippi*.

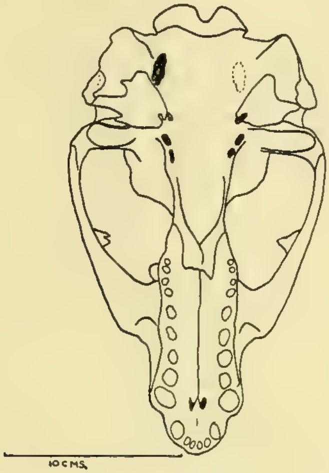


FIG. 3. Type skull of *Arctocephalus townsendi*, U.S. Mus. No. 83,617. Taken from Allen, 1905, Patag. Exp. III ; pl. xviii.

Merriam lists the most important characters for identifying the skull of *A. townsendi* as follows :

1. The exceedingly narrow and excavated palate.
2. Flat tympanic bullae.
3. Short and thick ascending arm of premaxilla.
4. Broadly expanded zygomatic root of maxilla, forming a floor under the anterior half of the orbit.
5. The 5th molar mainly posterior to the plane of the anterior root of the zygoma.

When these characters are compared with those given by Peters for the type skull of *A. philippi* it will be seen that Merriam's Nos. 1, 2 and 4—important diagnostic features—correspond exactly with Nos. 1, 4 and 3 respectively of Peters' description. Merriam's character No. 3 is not visible in the ventral view of the skull which he gives. His fifth character, while it is good for the specimen of *A. philippi* in the British Museum collection, is not distinctive.

When a further comparison is made between the measurements and proportions of the type skull of *A. philippi*, the skull of this species in the British Museum, and the type skull of *A. townsendi* (Table III) it will be seen that these three skulls are so similar that it is probable that they all belong to the same species of *Arctocephalus*. Comparison of the drawings (Figs. 1 and 3) of these skulls also confirms this view, and it is thus possible to add *Arctocephalus townsendi* Merriam to the synonymy of *Arctocephalus philippi* Peters.

Allen (1905) described skulls from the Galapagos which he called *A. philippi*, and combined a very " free translation " of the characters given by Peters with some which are obviously only from the skulls he was describing. His figured skulls show the typical high sagittal crest of the male *Zalophus* and it is clear that he has mistakenly identified these skulls as *A. philippi*. Osgood (1943) says that Remington Kellogg and G. M. Miller examined Allen's skulls from the Galapagos and found that they were undoubtedly *Zalophus californianus*.

TABLE III.

(See notes on measurements used)

	A. townsendi *type*		*A. philippi* *type*		*A. philippi* 1883.11.8.1	
	mm.	%	mm.	%	mm.	%
Greatest length	256		236		255	
Condylo-basal length	*252	100	233	100	248	100
Zygomatic breadth	151	59·9	129	55·4	139	56·0
Snout length	†69	27·4	63	27·0	73	29·4
Snout width at canines	†53	21·0	45	19·3	45	18·1
Canine to last upper molar (inclusive)	88	34·9	‡75	32·2	91	36·7
Distance between 3rd upper molars (internally)	22·5	8·9	21	9·0	19	7·7
Antero-posterior width of zygomatic root of the maxilla	21	8·3	20	8·6	22	8·9
Interorbital width (posterior to supra-orbital process)	†30	11·9	30	12·9	31	12·5
Mastoid breadth	†133	52·8	115	49·4	125	50·4
Greatest length nasals	—	—	41	17·6	45	18·1
Anterior breadth nasals	—	—	26	11·2	25	10·1

* Estimated.

† Measurements taken from 1/1 drawing of type skull in Allen (1905). Other measurements as given by Merriam (1897).

‡ Peters' type has only 5 upper molars. Measurements of skull taken from 1/1 drawing in Peters (1866).

DISTRIBUTION AND PARTIAL RECORDS OF *A. PHILIPPI* ON THE PACIFIC COAST OF AMERICA

The records of the occurrence of *A. philippi* which are listed below are based partly on the identification of actual specimens, and partly on records of " fur seals " from the Californian Islands which are, according to Starks (1922) *A. townsendi* = *A. philippi.*

1. *Juan Fernandez*

(*a*) 1864. Type specimen killed (Peters, 1866).
(*b*) — " Some years ago," possibly in 1864, a few dozen skins taken by Philippi (Philippi in Peters, 1871).
(*c*) 1883. Skull of specimen in British Museum collection. Presented by Chilean Government.
(*d*) — Skull in Santiago Museum. No locality given (Philippi in Peters, 1871).

2. *Masafuera*

(*a*) 1870. 3 seals collected. One of these described as type of *O. argentata* (Philippi in Peters, 1871).

3. *Chonos Islands*

(*a*) 1871. A skin taken by Philippi's assistant (Philippi in Peters, 1871).

4. *San Benito Islands*

(*a*) 1806. 8,338 skins taken by the " Port au Prince " (Townsend, 1924, 1931).

5. *Guadalupe*

(*a*) 1878. A few hundred skins taken from Guadalupe and Santa Barbara (Starks, 1922).
(*b*) 1880. Fur seals tightly packed (Merriam 1897).
(*c*) 1883. 2,000 killed, but commercially extinct (Merriam, 1897).
(*d*) 1891. Only a few seen (Merriam, 1897).
(*e*) 1892. 7 seals seen and 4 skulls obtained from which type of *A. townsendi* described (Merriam, 1897).
(*f*) 1922. None seen (Anthony, 1925).
(*g*) 1922. 2 year old female sent to San Diego Zoo (Starks, 1922).
(*h*) 1928. 2 males caught and sent to San Diego Zoo, and 60 seals estimated to be on the island (Townsend, 1931).
(*i*) 1929 . Some fur seals seen in May (Townsend, 1930).
(*j*) 1950. None seen (Bartholomew and Hubbs, 1952).

6. *Santa Barbara Islands*
   - (*a*) 1878. A few hundred skins taken from Guadalupe and Santa Barbara (Starks, 1922).
   - (*b*) 1890. 5 seals taken off San Miguel (Starks, 1922).
   - (*c*) 1901. 3 seals killed on Santa Cruz (Starks, 1922).
   - (*d*) 1949. Single adult male seen (Bartholomew and Hubbs, 1952).

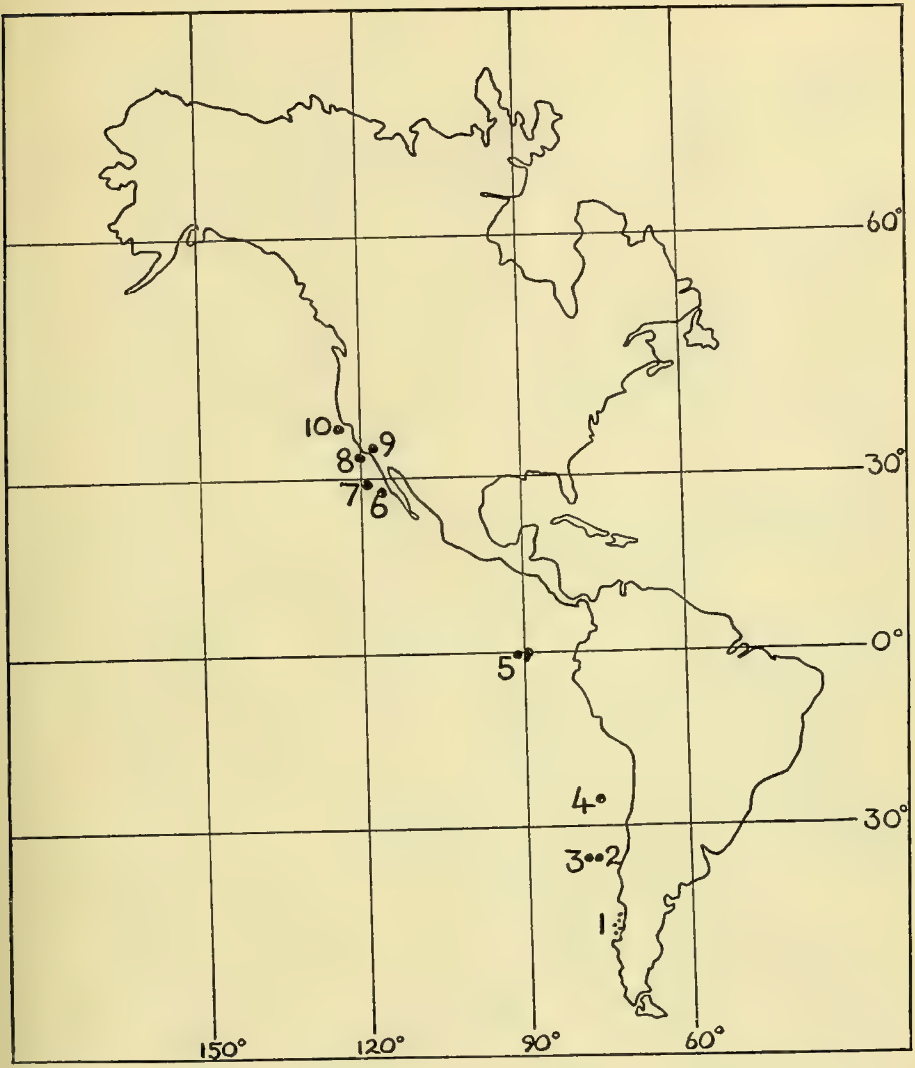
7. *Ventura, California*
   - (*a*) Eighteenth to nineteenth centuries. Abundant remains found in shell mound (Lyon, 1937).

8. *Farallone Islands*
   - (*a*) 1810–1812. 73,402 skins taken by Americans (Starks, 1922).
   - (*b*) 1812–1840. Russians took 1,200–1,500 skins annually (Starks, 1922).
   - (*c*) 1818. Seals diminishing rapidly (Starks, 1922).
   - (*d*) 1824. Seals profitable again, over 1,000 skins taken, but decreased to 54 skins in 2 years (Starks, 1922).

The first record of a relatively recent occurrence of the fur seal is the finding of skull remains from the eighteenth to nineteenth centuries in a shell mound at Point Mugu, Ventura County, California, 1,557 identifiable bones of this seal were found and it was by far the most abundant animal in the collection. No more records are available until 1806 when over 8,000 skins were taken from the San Benito Islands. The seal was abundant on all the islands off the Californian coast and was taken for its fur in great numbers until about 1883 when it was considered extinct commercially. From that time until the present day there have been only a few sporadic noted occurrences, the last being an adult male seen on San Nicolas Island in 1949.

As there are so few records of *A. philippi* being seen on Juan Fernandez and Masafuera it seems probable that the normal habitat of this seal is the islands off the Californian coast. When it is known to have been so plentiful in the northern part of its range it is noteworthy that there have been so few records of its occurrence on Juan Fernandez, although this may be attributed partly to the remoteness of this island compared with those off the Californian coast. It is probable that Juan Fernandez represents the most southerly extent of its distribution and that there has never at any time been a great number of *A. philippi* on the island. The presence of a small number of *A. philippi* would be masked by the large numbers of *A. australis* which undoubtedly occurred on the island, and the differences would not be noticed by the sealers who would class them all as " fur seals." It was only scientifically interested people like Dr. Philippi who collected the type which was named after him, and the chemist Fr. Leyboldt who collected the type of *O. argentata* who noticed the difference between the two species.

The present state of *A. philippi* is unknown. It may be extinct, but since an adult male has been seen as recently as 1949 it seems possible that there may still be a small colony left.



Map to show seal-inhabited islands off the Pacific American coast.

1. Chonos Islands.
2. Juan Fernandez.
3. Masafuera.
4. St. Felix, St. Ambrose, St. Mary's Islands.
5. Galapagos Islands.
6. San Benito Islands.
7. Guadalupe.
8. Santa Barbara Islands.
   San Nicolas.
   Santa Cruz.
   Santa Rosa.
   San Miguel.
9. Ventura.
10. Farallone Islands.

PARTIAL RECORDS OF "FUR SEALS" OFF THE COAST OF SOUTH AMERICA

1. *Masafuera*

(*a*) 1563. Island discovered. Swarming with fur seals (Allen, 1899).
(*b*) 1792. Capt. Stewart of the "Eliza" took 38,000 skins to Canton and sold them for 16,000 dollars (Allen, 1899).
(*c*) 1797. Americans came about this time. 2–3 million seals on island. 3 million taken to Canton in 7 years. People from 14 ships on island at the same time, all killing seals (Allen, 1899).
(*d*) 1798. Capt. Fanning of the "Betsy" took 100,000 skins to Canton and estimated that when he left there were still 500,000–700,000 seals on the island (Allen, 1899).
(*e*) 1807. Capt. Morrell—business scarcely worth following (Allen, 1899).
(*f*) 1824. Capt. Morrell—island almost entirely abandoned by seals (Allen, 1899).
(*g*) 1891. Capt. Gaffney saw 300–400 and took 19 (Allen 1899).

2. *Juan Fernandez*

(*a*) 1683. Dampier—seals thick about the island (Allen, 1899).
(*b*) 1687–90. Capt. Davies of the "Bachelors Delight" left some men on the island to cure seal-skins (Albes, 1914).
(*c*) 1741. Anson—many seals and sea-lions (elephant seals) (Anson, 1744).
(*d*) 1800. Capt. Delano—human population of 3,000 on island, so no seals left (Allen, 1899).
(*e*) 1891. Capt. Gaffney saw a few fur seals in December (Allen, 1899).
(*f*) 1931. Nybelin got a parasite from an *A. australis* (Nybelin, 1931).

3. *St. Felix, St. Ambrose, St. Mary's Islands*

(*a*) 1792. 13,000 skins taken during August and September by American ship "Jefferson" (Howay, 1930).
(*b*) 1801. Islands were visited by sealers and there must have been large numbers of seals (Allen, 1899).
(*c*) 1816. Capt. Fanning took 14,000 skins at St. Mary's (Allen, 1899).
(*d*) 1891. No seals worth mentioning (Allen, 1899).

4. *Galapagos Islands*

(*a*) 1535. Seals mentioned by discoverer of Galapagos (Baur, 1897).
(*b*) 1800. Large numbers of fur and hair seals (Allen, 1899).
(*c*) 1816. Capt. Fanning took 8,000 fur seals and 2,000 hair seals (Allen, 1899).
(*d*) 1825. Capt. Morrell took a few fur seals from Albemarle (Allen, 1899).
(*e*) 1872. Capt. Reed took 3,000 fur seals and about as many more during three subsequent voyages between 1872 and 1880 (Allen, 1899).

(*f*) 1872. Hassler Expedition. Specimens of *A. australis* collected (Allen, 1880).
(*g*) 1885. Capt. Gaffney took 1,000 fur seals (Allen, 1899).
(*h*) 1898–99. Capt. Noyes—seals not very numerous, took 224 skins (Allen, 1899). Heller collected type of *A. galapagoensis* on this voyage (Heller, 1904).
(*i*) 1923. Beebe saw only two fur seals (Beebe, 1924)
(*j*) 1931. Sea-lions and seals numerous and quite tame (Korwin, 1931).
(*k*) 1932–33. Capt. Hancock caught several fur seals which were presented to San Diego Zoo (Townsend, 1934).

As even the incomplete list above shows, there is quite a number of records of sealers taking fur seals from the islands off the South American coast from the Galapagos Islands southwards. The story of these fur seals is the usual one of uncontrolled exploitation. Millions of skins were taken until the middle of the nineteenth century when the numbers dropped rapidly and for about the last 40 years not only are there no records of any commercial sealing, but there are very few referring to seals at all, and even these indicate that there cannot be many fur seals on the islands.

It appears from the available records that the sealing expeditions worked northwards along the west coast of South America, as seals at Masafuera and Juan Fernandez were abundant until about 1798, at St. Mary's until 1816, while there were still considerable numbers at the Galapagos as late as 1885.

There is still some doubt as to the identity of these " fur seals." Townsend (in Allen, 1899) refers to the Galapagos seal as *A. philippi*, but does not give any reasons for his identification. The only other records where specific names are used are those of Allen (1880), Heller (1904), Nybelin (1931) and Townsend (1934) for seals on the Galapagos and Juan Fernandez and in all four instances *A. australis* is the animal named. Both *A. australis* and *A. philippi* have been reliably recorded from Juan Fernandez, and *A. australis* from the Galapagos, so it is not unlikely, though not proven, that *A. philippi* also occurs on the Galapagos. The bulk of the records of " fur seals " from these South American islands probably refer to *A. australis* although the scarcity of records makes it impossible to be certain. For the same reason it is not known what the present status of this seal is along the western South American coast.

Other Otariids frequent the shores and islands of the Pacific coast of America. Of these the best known is the Californian sea-lion *Zalophus californianus*. The most southerly point from which it has been recorded is the Galapagos Islands. Beebe (1924) went to these islands in 1923 and makes several references to the sea-lions that he saw there. He identifies them as " Southern sea-lion, *Otaria jubata*," but the photographs he gives show the short pointed nose of *Zalophus* and not the heavy upturned snout of *O. byronia*. Wollebaek (1927) went to these islands in 1925, and although he does not mention the seals by name he gives a photograph which is undoubtedly of a *Zalophus*. Skulls of *Zalophus* from the Galapagos which are in the U.S. National Museum are figured by Allen (1905) although he wrongly calls them *A. philippi*. *Zalophus* is well known on the islands off the Californian coast and probably extends northwards as far as the bay of San Francisco.

Steller's sea-lion, *Eumetopias jubatus*, is known to extend its range as far south as San Nicolas Island, although there are no records of it breeding any further south than Santa Rosa Island, 42 miles north of San Nicolas.

The Northern fur seal *Callorhinus ursinus*, although it breeds mainly on the Pribilof Islands, spends the winter and early spring at sea and may migrate southwards to the latitude of California, although it rarely comes ashore there.

The distribution of the Southern sea-lion, *Otaria byronia*, corresponds with that *of A. australis*. Both Heller (1904) and Allen (1880) note its presence on the Galapagos Islands and it is known on Juan Fernandez, round Cape Horn and along the eastern coast of South America as far as Lobos Island, Uruguay.

SUMMARY OF THE MAIN CHARACTERS AND DISTRIBUTION OF THE OTARIIDS OF THE PACIFIC COAST OF AMERICA

Otaria byronia Blainville, 1820. Southern sea-lion.

Size. Length of adult male from nose to end of tail 6–7 ft., and of female 5–6 ft. Weight of adult male over 1,500 lb.

Description. Males and females similar in colour, back usually dark brown, mane of male and neck of female, and the belly dark yellow. Face dark and hair of flippers reddish. Bare parts of skin black. Whiskers long, reaching 12 in. in adult male, about 30 on each side, straw coloured and forming a pale moustache. Variations in colour frequent, and many paler animals found. Newly-born pups practically black, soon fading to chocolate, and after first moult at a few months old, a dark grey.

Male with extremely thick and heavy neck thrown into folds, this together with the lighter and thicker hair on the neck gives the appearance of a mane. Female slighter in build. Head short and muzzle deep and upturned.

Distribution. From Lobos Island, Uruquay to Straits of Magellan, Falkland Islands, Galapagos Islands.

Skull. Condylo-basal length up to 358 mm. in adult males, and 267 mm. in adult females. Easily distinguishable from skulls of all other seals by the greatly elongated palate extending backwards as far as the pterygoids, and becoming progressively more concave posteriorly. Adult male skull with well-developed sagittal and parietal crests, and various processes on the parietal for the attachment of muscles.

Dentition. $\text{i.}\frac{3}{2}\ \ \text{c.}\frac{1}{1}\ \ \text{m.}\frac{6}{5}.$

Eumetopias jubatus (Schreber 1776). Steller's sea-lion.

Size. Length of adult male from nose to end of tail 11–13 ft. and of adult female 8–9 ft. Weight of adult male 1,000–1,200 lb., of adult female 400–500 lb.

Description. Both males and females a light reddish brown ; slightly darker on the belly. Colour varying with age and season and coat lighter when just moulted. Naked parts of skin black. Whiskers long and slender, the longest about 20 in., white or brownish white. Adult males with mane on neck. The largest of the eared seals. Has a rather bear-like head with a short straight nose, not upturned as in *O. byronia.* Muzzle and neck very heavy.

Distribution. Shores of the north Pacific from Behring Straits southward to Santa Barbara Islands, California, and Japan.

Skull. Condylo-basal length up to 380 mm. in adult males. Skull distinguished by the anteriorly placed quadrate supraorbital processes and, in all except young skulls, a large gap between the upper 4th and 5th molars. Palate with hinder end contracted and truncate.

Dentition. $i.\frac{3}{2}$ $c.\frac{1}{1}$ $m.\frac{5}{5}$.

Arctocephalus philippi (Peters 1866). "Juan Fernandez" fur seal.

Size. Length of adult male from nose to end of tail *ca.* 5 ft. Adult female probably slightly smaller.

Description. Above blackish grey, more yellowish grey on head and neck; brownish black below, proximal part of limbs, lips and chin rusty brown. Overhair rusty brown with black tips, thick underfur rust red. Whiskers in six rows, some black, some white, and some white with black tips. Animal distinguished by slender tapering snout.

Distribution. Juan Fernandez, Guadalupe, Santa Barbara Islands, Farallone Islands.

Skull: 1. Skull narrow, the mastoid breadth being 48–50% of condylo-basal length.
2. Palate narrow and very deep in front.
3. Maxillary root of zygoma very wide.
4. Flat tympanic bullae.
5. Narrow zygomatic arch.
6. Snout narrow.
7. Posterior prolongations of palatines not thickened.
8. Teeth usually without accessory cusps and widely spaced.

Measurements of few authentic specimens known but condylo-basal length of adult male skull *ca.* 256 mm.

Dentition. $i.\frac{3}{2}$ $c.\frac{1}{1}$ $m.\frac{6}{5}$. (Peters' type skull has only $m.\frac{5}{5}$ but number of molar teeth of *Arctocephalus* rather variable).

Arctocephalus australis (Zimmermann 1783). Southern fur seal.

Size. Length of adult male from nose to end of tail 5 ft. 6 in., and of adult female 4 ft.

Description. Overhair black, tipped with grey except on belly where blackish brown. Hairs 1–2 in. long on back of neck but shorter over rest of body. Underfur reddish brown. Dorsal surface of manus and pes covered up to nails with black hairs. Tip of nose and naked skin of limbs black. Whiskers white, though some of the smaller are greyish black, about 20 on each side. Very few photographs available, but appears to be rather like *Callorhinus* in the external shape of the head, except that the nose is rather longer and slightly upturned.

DISTRIBUTION. Shores and islands of South America from Lobos Islands, Uruguay, to the Galapagos Islands, Straits of Magellan, Falkland Islands, S. Georgia.

SKULL. Condylo-basal length up to about 250 mm. in adult male. Skull squarish in general shape, heavily built, with thick zygomatic arches and short broad nasals.

DENTITION. i.$\frac{3}{2}$ c.$\frac{1}{1}$ m.$\frac{6}{5}$.

Callorhinus ursinus (L.). Northern fur seal.

SIZE. Length of adult male from nose to the end of tail 7–8 ft. and of adult female 4ft. Weight of adult male 500–600 lb., of adult female 80–100 lb.

DESCRIPTION. Males nearly black on the back and brownish ventrally, neck and shoulders greyish. Limbs reddish brown. Naked areas of skin black. Females lighter than males. being grey dorsally, but otherwise like males. Whiskers white, or with brownish tips. Black in young animals. Distinguished externally by the high forehead and extremely short pointed nose.

DISTRIBUTION. From Pribilof Islands south to California and Japan.

SKULL. Condylo-basal length up to *ca.* 250 mm. in adult males. Interorbital region long, facial region very short and high, descending abruptly. Dentition weak.

DENTITION. i.$\frac{3}{2}$ c.$\frac{1}{1}$ m.$\frac{6}{5}$.

Zalophus californianus (Lesson 1828). Californian sea-lion.

SIZE. Length of adult male from nose to end of tail 8 ft., and of adult female 6 ft. Weight of adult male 500–600 lb.

DESCRIPTION. Not so heavily built as *Otaria* or *Eumetopias* with not such a thick neck in adult males.

DISTRIBUTION. Galapagos (but see Sivertsen's (1953) account of *Z. wollebaeki*), shores and islands of California north to Farallone Islands.

SKULL. Condylo-basal length up to 320 mm. in adult males. Skull of adult males easily distinguishable by the very high sagittal crest. Skulls of females and young males slender with elongated nasals and facial regions.

DENTITION. i.$\frac{3}{2}$ c.$\frac{1}{1}$ m.$\frac{6}{5}$.

KEY FOR DISTINGUISHING SKULLS OF PACIFIC AMERICAN OTARIIDAE

1. Skull with supraorbital processes and alisphenoid canal . . . . . . *Otariidae*
    2. Posterior end of floor of palate very concave and extending backwards as far as the pterygoids . . . . *O. byronia*
    2a. Posterior end of floor of palate not extending backwards as far as the pterygoids 3.
        3. Supraorbital processes quadrate. Molars 5/5 with large gap between upper m. 4 and m. 5 in adult skulls . . . . *E. jubatus*

3*a*. Supraorbital processes triangular. Molars 6/5 with no large gap between upper m. 4 and m. 5 in adult skulls . . . . 4.
4. Nasals long and slender, combined widths at anterior ends *ca.* 40–50% of length 5.
4*a*. Nasals short and broad, combined widths at anterior ends *ca.* 80–90% of length 6.
5. Palate very narrow, the internal distance between m. 1–3 being the same. Floor of palate very concave between these molars. Tympanic bullae smooth and rounded. No very high sagittal crest in old males . *A. philippi*
5*a*. Palate wider, the distance between the molars increasing gradually. Floor of palate only very slightly concave. Surface of tympanic bullae irregular. Very high sagittal crest in old males . . . *Z. californianus*
6. Interorbital region long in adult animals, *ca.* 20% of condylo-basal length. Snout, at level of m. 2, practically as high as it is long . . . *C. ursinus*
6*a*. Interorbital region less than 20% of condylo-basal length in adult animals. Snout much longer than it is high . . . . . . *A. australis*
1*a*. Skull without supraorbital processes or alisphenoid canal (not considered in this key) *Phocidae*

Note : The above characters apply mainly to adult skulls.

SUMMARY

After comparison with skulls of fur seals known to occur along the Pacific coast of America, the type skull of *Arctocephalus galapagoensis*, which was collected on Wenman Island in the Galapagos group in 1898–99, is shown to be similar to skulls of *A. australis.*

Skulls of fur seals brought back from the Galapagos Islands in 1932–33 are also identified as *A. australis.*

A statistical treatment of proportions of skull measurements of *A. australis* from the Falkland Islands on the one hand, and the mainland of South America and the Galapagos Islands on the other, makes it seem probable that the Falkland Islands animals belong to a larger race. The shortage of specimens makes it impossible at the moment to distinguish the Galapagos skulls from those of other mainland populations.

It is shown by a comparison of skull drawings, measurements and proportions that the Guadalupe fur seal *A. townsendi* is the same as the Juan Fernandez fur seal *A. philippi.* A chronological list is given of the recorded occurrences of this seal and it is suggested that its normal habitat is the islands off the coast of California. The few records from Juan Fernandez represent animals taken at the most southerly point of the range, but its abundance there was probably masked by the greater numbers of *A. australis.*

A list is given of records of un-named " fur seals " from the Galapagos Islands southwards. It is probable that most of these records refer to *A. australis.*

A brief account is given of the distribution of *Z. californianus*, *E. jubatus*, *C. ursinus* and *O. byronia*, the other Otariids which occur along the coast.

A summary is given of all the Otariids occurring along the Pacific coast of America, and also a key for distinguishing their skulls.

ACKNOWLEDGMENTS.

I wish to express my indebtedness to Professor G. S. Myers and Mr. J. M. Savage of Stanford University, California, for the assistance they have given me by supplying

information and measurements relating to the type skull of *A. galapagoensis*, and also to Dr. Antenor L. de Carvalho, Museu Nacional, Rio de Janeiro, who took the photographs of this skull reproduced in the text, while working in Stanford University.

NOTES ON THE MEASUREMENTS USED

1. Greatest length—from the posterior surface of the occipital condyles to the anterior surface of the knob formed by the premaxillae, above the incisors.

2. Condylo-basal length—from the posterior surface of the occipital condyles to the anterior surface of the premaxillae at the level of the incisors.

3. Snout length—from the most anterior part of the edge of the orbit to the anterior surface of the premaxillae at the level of the incisors.

4. Antero-posterior width of the zygomatic root of the maxilla—between the inferior lip of the antorbital foramen and the orbit.

5. Gnathion—is defined by Thomas (1905) as the most anterior point of the premaxillae, on or near the mid line. In *Arctocephalus* the most anterior point of the premaxillae is a projecting knob of very variable size, so the gnathion is taken here as the most anterior surface of the premaxillae at the level of the incisors, and does not include the knob.

6. Basion—as defined by Thomas (1905), a point in the middle line of the hinder edge of the basioccipital margin of the foramen magnum.

7. Henselion—as defined by Thomas (1905), the back of the aveolus of either of the median incisors.

8. Palation—as defined by Thomas (1905), the most anterior point of the hinder edge of the bony palate, whether in the middle line or on either side of a median spine.

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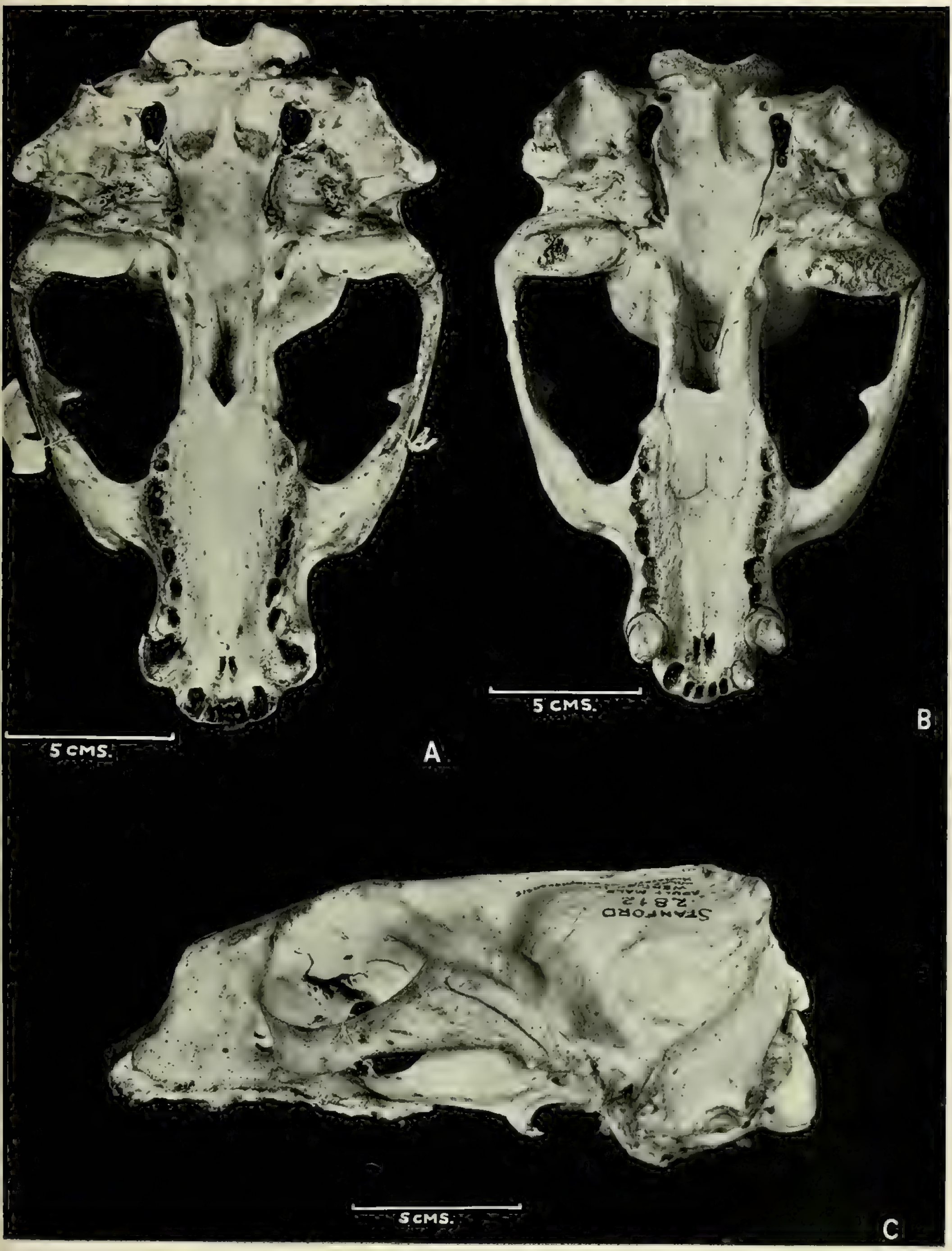
PLATE 10

A. Ventral view of type skull of *Arctocephalus galapagoensis*, No. 2812, Stanford University, California. (Photograph by Dr. Antenor L. de Carvalho.) B. Ventral view of skull of *A. australis*, 1880.7.28.7, B.M.(N.H.). C. Lateral view of type skull of *A. galapagoensis*, No. 2812.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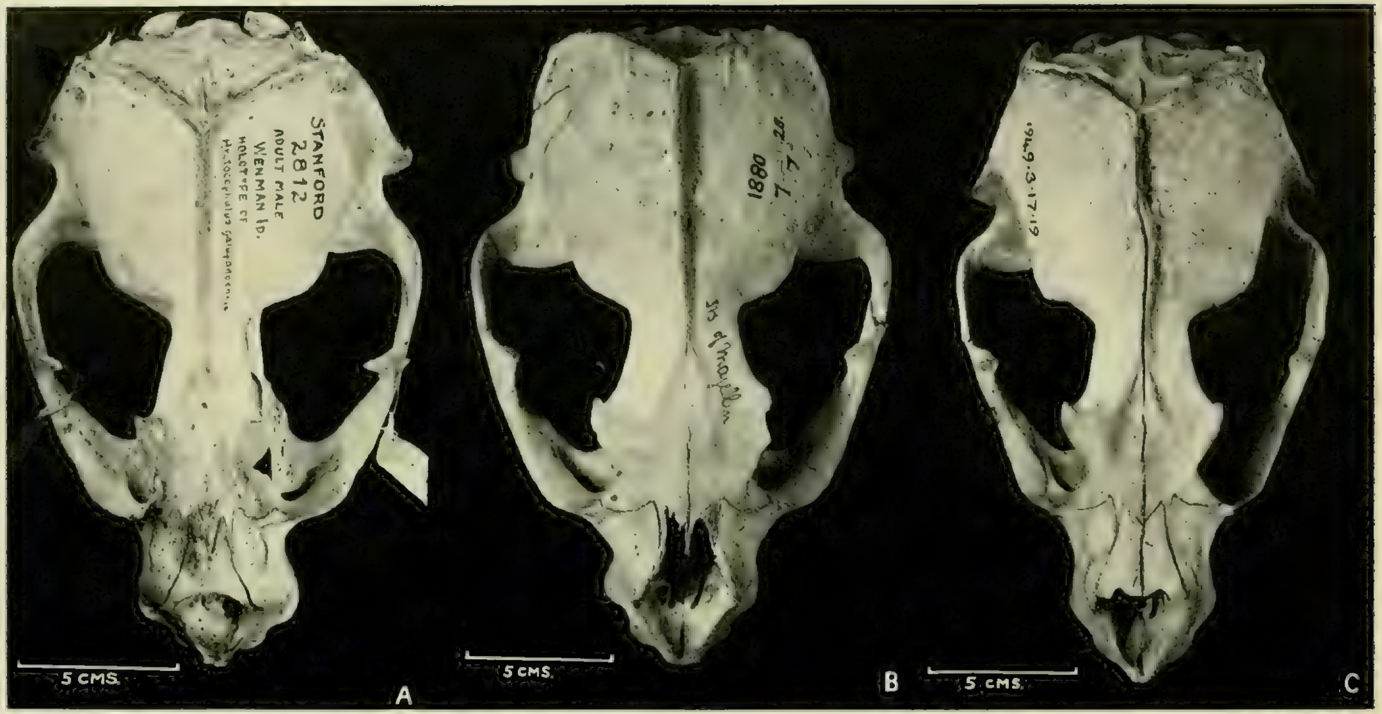
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PLATE 11

Dorsal views of: A. Type skull of *A. galapagoensis*, No. 2812. B. Skull of *A. australis*, 1880.7.28.7, B.M.(N.H.). C. Skull of *A. australis*, 1949.3.17.19, B.M.(N.H.). B and C are skulls of *A. australis* of the same condylo-basal length from the Straits of Magellan and the Falkland Islands respectively.

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THE SOUTHERN RIGHT WHALE DOLPHIN, *LISSODELPHIS PERONI* (LACÉPÈDE)

28 JAN 1955
PRESENTED

F. C. FRASER

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THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 2 No. 11
LONDON: 1955

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BY

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Pp. 339–346; *Pl.* 12; 1 *Text-figure*

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THE SOUTHERN RIGHT WHALE DOLPHIN, *LISSODELPHIS PERONI* (LACÉPÈDE)

EXTERNAL CHARACTERS AND DISTRIBUTION

By F. C. FRASER

EARLY in 1952 three dolphins became stranded on the beach at Onekaka, Golden Bay, which is at the northern end of South Island, New Zealand. Mrs. G. J. Goulter of Golden Bay took an 8 mm. colour film of the animals, all of which were alive. They were eventually returned to the sea and swam away apparently none the worse for their temporary sojourn on dry land. I wish to express my thanks to Mrs. Goulter for her permission to let prints be made of three of the frames of the film and also to her brother, Captain R. E. Washbourn, R.N., who brought the film to the British Museum and helped in the subsequent arrangements for pictures from it to be used in the present note.

It was clear as soon as the film was projected that the dolphins belonged to the species *Lissodelphis peroni*, the Southern Right Whale Dolphin, and although this species has been recognized for a century and a half I am not aware that any photographic record of it has previously been published. The photographs (Pl. 12) show the characteristic external features of this species, the most noteworthy of course being the absence of a dorsal fin and the spectacular coloration of the body. The pictures of the three animals resting on the sand (Pl. 12) suggest that they unlike most dolphins, are broader than deep in the thoracic region. While this appearance may only be due to the shape assumed by the body when not waterborne, it is possible that it may be natural and is perhaps a stabilizing factor in an ocean-going dolphin which lacks a dorsal fin. The slender tail stock can be seen and, although none of the pictures reproduced here gives a good impression of the pectoral fins, inspection of the whole film indicated that their shape is, as in very many of the Delphinidae, with shallowly convex anterior border and with the hinder margin convex proximally and concave distally. The head is seen to taper to a snout which, laterally, is well defined from the " forehead " by an angular depression shallowing as it approaches the middle plane of the head, so that in the profile of the head the " forehead " merges into the rostrum with only the slightest indication of a break in the line. The tip of the lower jaw protrudes to a noticeable distance beyond that of the upper.

The dorsal surface of the body is of a bluish-black colour which is sharply demarcated from the glistening white ventral region. Snout, forehead and lower jaws are white ; the blowhole and eyes come within the pigmented area. From the top of the head, where the pigment extends anteriorly in a little peak, the boundary between black and white sweeps low down on the lateral surface of the thorax, reaching its lowest limit about the insertion of the flippers, which have their origin in the unpigmented region. The boundary then takes an upward direction until about half the depth of the body is reached in the lumbar region. Thence it continues caudad about midway between the dorsal and ventral margins of the body. A close inspection of the film was made to decide about the dorsal surface of the tail flukes. Some indication of the amount of pigment on the tail of one of the specimens can be obtained from Pl. 12, fig. 3, but allowance has to be made for the high-light which gives an impression of a lightness of pigmentation not present in the animal itself. While in the specimen just referred to the colour was grey-blue, in one at least of the remaining two the dorsal surface of the flukes was of exactly the same bluish-black colour as the back. In addition it was seen in the film that the posterior margin of the white ventral surface of the flukes was bordered by a thin band of dark pigmentation in one specimen, while in another the band was appreciably wider, about an inch at its widest. There was definite evidence in part of the film that, although at first sight the flippers appeared altogether white, at least one of the animals had a narrow elongated darkly-pigmented patch filling the apex of the proximal convexity on the posterior border of the limb.

The first published description of *L. peroni*, that of Lacépède (1804) includes comment on the contrast of the dark colour of the back with the brilliant white of the sides and belly and with that at the end of the tail, the extremity of the snout and on the flippers.

Lesson (1827) gives a more detailed account of the external appearance of this species of dolphin. " Arrondi dans ses contours, gracieux dans ses formes, lisse dans toutes ses parties, ce cétacé est d'autant plus remarquable, qu'il semble recouvert d'un camail noir. Son museau jusqu'à l'oeil est d'un blanc soyeux ou argentin. Il en est de même des côtés du corps, des nageoires pectorales, du ventre et d'une partie de la queue. Un large scapulaire, d'un bleu-noir foncé, prenant naissance aux yeux où le blanc décrit un croissant, se dessine et se recourbe sur les flancs, pour recouvrir seulement la partie supérieure du dos. Le bord antérieur des nageoires pectorales et caudales est brun. Le museau est allongé, séparé du crâne par un sillon profond." The figure of the specimen (Lesson's Pl. 9, fig. 1) does not convey the elegance of form expressed in the description and in particular the shape of the attenuated snout is quite unlike that of the animals photographed in New Zealand.

Bennett (1840) says : " The upper and hind part of the head, the back, and flukes are of a uniform deep-black colour which about the lower third of the body, terminates by a straight and abrupt line, leaving the entire abdomen, and inferior portions of the sides, of a pure and dead white. The snout, and anterior third of the head, are entirely white ; as also are the swimming paws, with the exception of a broad black spot on the upper surface and posterior margin of each." Bennett's figure is of an animal with a disproportionately large head and a body deep in comparison with its length.

Gray (1846) quotes Cuvier's criticism of the snout shape as depicted by Lesson and on his own account draws attention to the restriction in the latter's figure of the pigmented dorsal part of the body. He reproduces drawings made at sea which in these essentials resemble the animals photographed in New Zealand. In Gray's figures the upper surface of the tail-flukes is of the same dark colour as the dorsal surface of the body. His lateral view of the dolphin shows the profile of the anterior end of the lower jaw continuing the line of the profile of the snout. This is not substantiated in the rounded lower jaw tip of the New Zealand animals.

D'Orbigny and Gervais (1847) have the briefest description of a specimen harpooned near Cape Horn. The drawing in their account shews an animal somewhat slender in form, with the conventional pattern of pigmentation on the dorsal surface of the body and having the dorsal surface of the flukes of the same black colour. In addition the dorsal surface of the snout has pigment on it which does not, however, extend to the margin of the upper jaw and stops short of the pigmentation on the top of the head. The flipper is shown bearing a large irregular black spot about the middle of the posterior edge, and on the tail stock, just anterior to the insertion of the flukes, four short oblique flecks of dark colour project ventro-caudally from the boundary which separates the black of the back from the white of the under surface.

Philippi (1893) describes two specimens caught off the east of Patagonia about 41° S. The figure which he gives of one of these indicates that, in general, the animal was like those described by earlier writers. Philippi says that the flippers were pure white above and below, only the rearmost corner and tip being black, and the tail black above, white below with black posterior border.

Lillie (1915) refers briefly to *L. peroni* having been seen twice, a pair of animals on each occasion. He states that all four were exactly alike and agreed with Gray's figure except that the tail flukes were quite white above and below.

Summing up the foregoing descriptions, it would appear likely that only one species of *Lissodelphis* is involved for which the name *L. peroni* has priority. The colour pattern is constant so far as it concerns the amount of black on the back and white on the belly but varies in the amount of pigmentation on the snout, flippers and on the dorsal surface and ventral margin of the tail flukes.

This colour pattern is clearly distinguishable from that of the northern form *L. borealis* (Peale). Excellent photographs of this northern species are to be found in the account of Scheffer and Slipp (1948). These show an animal which is much more extensively pigmented than its southern congener. In *L. borealis* the dark pigmentation covers the greater part of the body. The rostrum and anterior part of the " forehead " appear light grey in one of the photographs in the paper just referred to and the end of the lower jaw is without pigment. A roughly lozenge-shaped area of white lies between the flippers on the ventral surface of the body which, anteriorly, extends on to the throat, where it ends in a sharp angle. Posteriorly it is drawn out to become a thin white line in the umbilical region and thence to the tail it widens out again very gradually. The dorsal surface of the tail is black and the ventral surface white with a black band on the middle line and posterior border.

In the consideration of the geographical distribution of *L. peroni* it is convenient to start with the type locality and continue eastwards round the globe. Peron (1807) himself says that the species which bears his name was based on a specimen caught off the south coast of Tasmania ; on the day following the capture the ship's position was 44° S., 141° 27′ E. Flower and Garson (1884) record a skull which was sent to the Royal College of Surgeons from Tasmania. Lillie saw the dolphin on two occasions in positions 42° 51′ S., 153° 56′ E. and 47° 04′ S., 171° 33′ E. respectively, the former being eastward of Tasmania, the latter off the southern end of the east coast of South Island, New Zealand.

The three specimens which are the subject of the present paper stranded on the north end of South Island. The specimen figured by Gray (1846) was seen in position 46° 48′ S., 142° W. that is roughly halfway between New Zealand and the southern end of South America.

In the neighbourhood of Cape Horn, Malm's (1871) record of a skull from " Southern Chile " is not by itself very indicative as to exact locality but it may legitimately be mentioned in association with the other reports from the same region. Lesson (1827) saw the dolphin near Pillar Cape at the western end of the Straits of Magellan and says that on the 12th January, 1823, several hundred surrounded the " Coquille ", the ship then being three days south of the Chonos Archipelago, Chile, that is about 45° S. Bennett (1840) first saw specimens of *L. peroni* in 40° S., 50° W., south eastwards from the mouth of the Rio de la Plata. It was afterwards frequently seen by him during the passage round the Horn as far south as 54° S., but was not observed in lower latitudes than 40° S. on the western side of Cape Horn, nor indeed during any subsequent part of the voyage. Philippi's (1893) specimens, a male and a female, were caught off the east coast of Patagonia about 41° S. D'Orbigny and Gervais (1847) say it was observed around Cape Horn from 58° to 64° S. Mr. R. M. Laws (St. Catherine's College, Cambridge) to whom I am indebted for the record, has informed me that while on a passage from Monte Video to Stanley, Falkland Islands, he saw dolphins which were unquestionably *L. peroni*. The extract from his diary reads : " Jan. 22nd, 1948, 16·50 hours. A school of about 60 dolphins approached the ship from a S.E. direction. Some accompanied us for a few minutes. . . . There were two types, one greyish on top and white below with no definite line of demarcation and with a very pointed beak. It also had two parallel white lines along the flanks. (Probably *Lagenorhynchus obscurus*. F.C.F.). The other species was black and white clear cut, with *no* dorsal fin and having a white beak . . . a fix at 19.40 hours gave our position as 42° 2′ S., 56° 6′ W."

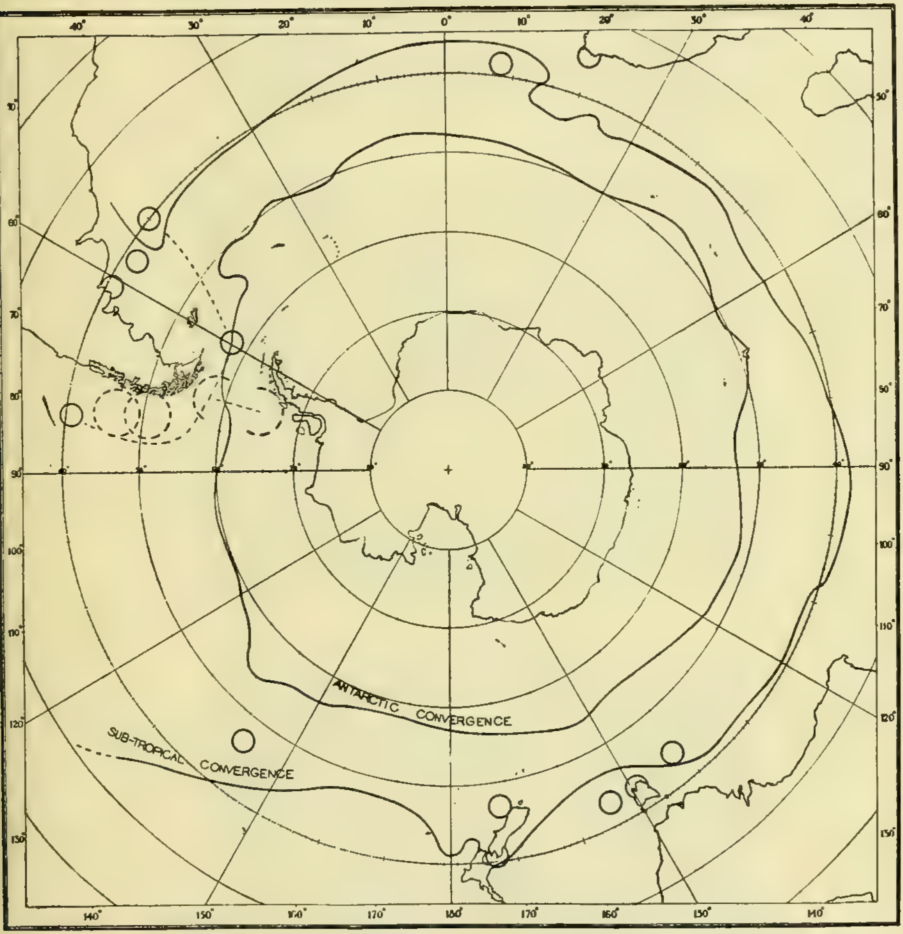
Eastwards across the South Atlantic at the southern end of the African continent two records are known. Schlegel (1841) refers to a skull which came from the Cape of Good Hope, but True (1889) is doubtful about the identity of this specimen. The other record is that of Dr. J. E. Hamilton, who in 1927 recorded and made a drawing of a dolphin which is certainly *L. peroni*, seen in position 38° 34′ S., 8° 06′ E.

The only remaining acceptable record, and it is not a very precise one, is that of Lesson (loc. cit.), who says that the dolphin " was seen in 45° S. in circumnavigating Australia."

Quoy and Gaimard (1824) refer to a dolphin with long white beak seen in 2° S. near New Guinea. This was distinguished as " delphinus Peroni de Lacépède ".

Neither this brief description nor the place of occurrence justifies acceptance of the record.

The well-substantiated places of occurrence of *Lissodelphis peroni* indicate that it probably ranges round the world in the southern hemisphere. Although it is not entirely restricted to the West Wind Drift it appears to have some predilection for it, because, as shown in Fig. 4, those records to the north of the Sub-tropical Convergence are for the most part close to that boundary, and except for one sight record there is no evidence that it penetrates into the Antarctic Ocean.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TEXT-FIG. 1. Distribution of *Lissodelphis peroni*. Complete circles indicate precise positions, dotted circles and lines indicate less well defined places of occurrence.

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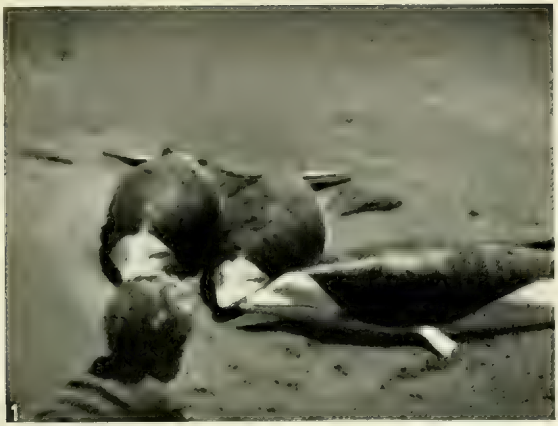
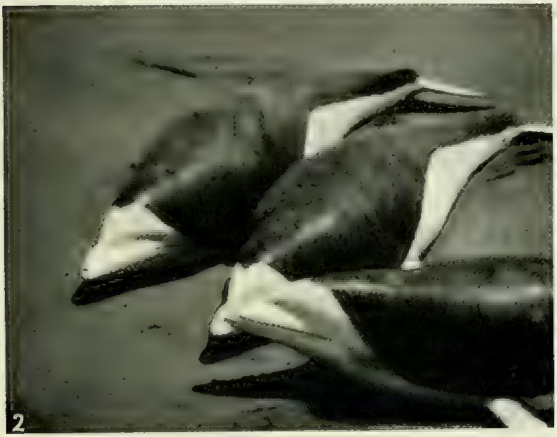
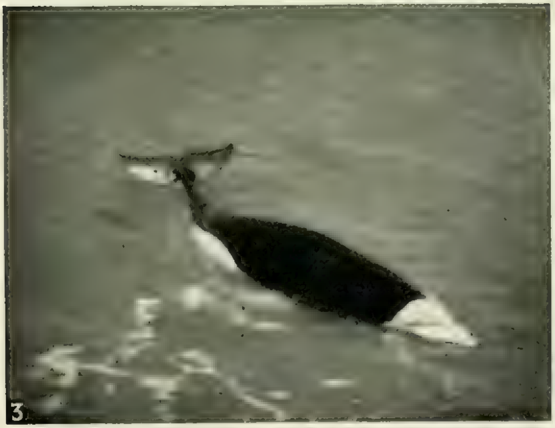
EXPLANATION OF PLATE

PLATE 12

Figs. 1–3. *Lissodelphis peroni.* Figs. 1 and 2. The dolphins on the beach at Onekaka, South Island, New Zealand. Fig. 3. One of the animals having been returned to the sea but not water-borne. (*Photo :* Mrs. G. L. Goulter).







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20 JUL
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NEW SPECIES OF *TILAPIA* (PISCES, CICHLIDAE) FROM LAKE JIPE AND THE PANGANI RIVER, EAST AFRICA

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SYNOPSIS

Three new species and one new subspecies of *Tilapia* are described from the Pangani River system. Field and pond observations are given, and also observations on the growth of *T. esculenta* Graham and *T. variabilis* Boulenger, collected as fry from Lake Victoria and reared in ponds.

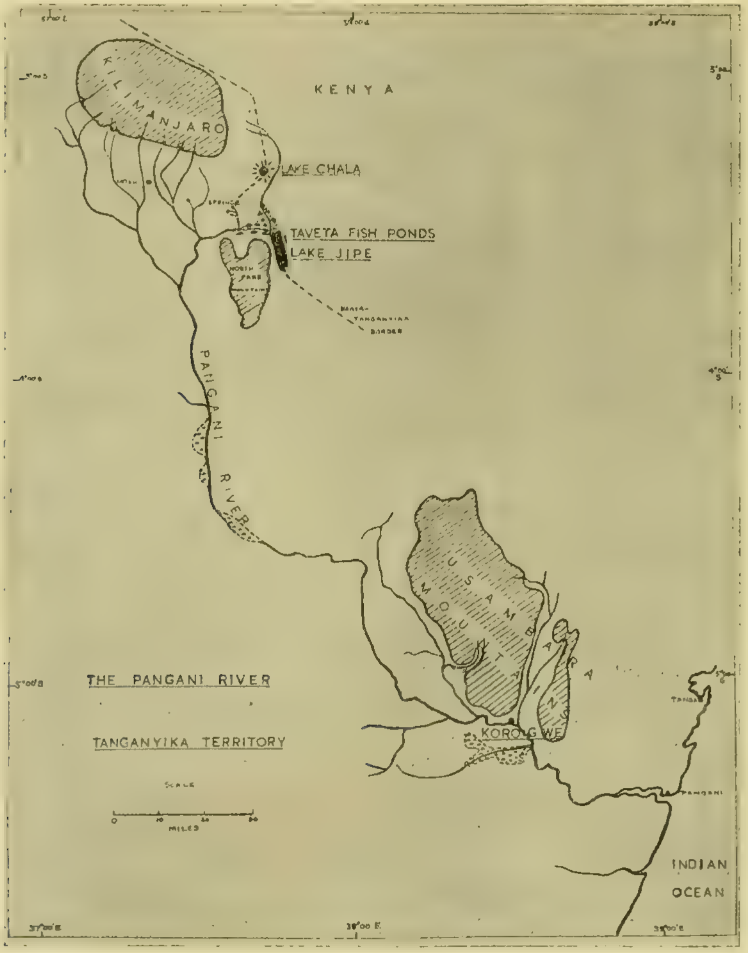
INTRODUCTION

In recent years recognition of the need for more protein in the diet of Africans has led to investigations of the growth of African fish in ponds. Certain species of Cichlid fishes of the genus *Tilapia* have proved very amenable to pond culture. This paper is concerned with an investigation, made in January, 1951, of the Tilapia species of the Pangani River system, certain of which were already being grown in fish ponds.

The Pangani River flows through Tanganyika Territory in a south-easterly direction from Lake Jipe, which lies on the Kenya border just south-east of Kilimanjaro, to the Indian Ocean (Text-fig. 1). Samples of Tilapia were collected from Lake Jipe, from ponds at Taveta near Lake Jipe, and from the Tanganyika Government's experimental fish farm at Korogwe. The Taveta ponds were stocked with fry from Lake Jipe. The Korogwe ponds were supplied with water by a channel leading from the Pangani River, and separate ponds were stocked with

Pangani River Tilapia and Lake Jipe Tilapia; Lake Victoria and Belgian Congo species foreign to the Pangani system had been introduced into other ponds at Korogwe.

Lake Jipe is connected with the Ruvu or Pangani River in wet seasons through a series of swamps. In 1951 the lake was about twelve miles long by one and-a-half miles wide, but was said to be silting up and spreading ; it was a shallow lake, only a few feet deep over much of its area, with large patches of water plants, *Potamogeton* and *Najas* species, rising to the surface, and frequented by numerous water birds.


KILIMANJARO
KENYA
LAKE CHALA
SPRINGS
TAVETA FISH PONDS
LAKE JIPE
KENYA-TANGANYIKA BORDER
PANGANI RIVER
USAMBARA MOUNTAINS
KOROGWE
TANGA
PANGANI
INDIAN OCEAN
THE PANGANI RIVER
TANGANYIKA TERRITORY
SCALE
0
10
20
30
MILES
5°00'S
37°00'E
38°00 E
39°00'E

TEXT-FIG. 1. The Pangani River system, Tanganyika Territory.

The Tilapia collected were examined at the British Museum (Natural History) together with other specimens from Lake Jipe collected previously by Mr. H. Copley, Fish Warden, Kenya, and from the Pangani River collected by Major R. E. Gould, Fisheries Officer i/c Fish Farming in Tanganyika Territory. The following Tilapias considered to be new and described below were found:

T. jipe sp. n. and *T. girigan* sp. n. in Lake Jipe ;
T. pangani sp. n. from the Pangani river at Korogwe ; and
T. mossambica korogwe subsp. n. from Korogwe ponds fed by the Pangani River.

Although, at first, resemblances to T. *mossambica* Peters and *T. nigra* Günther suggested that the Jipe and Pangani forms might find a place with these in one supraspecies, closer examination has emphasized the differences and, except for *T. mossambica korogwe* subsp. n., they are here described as distinct species, with some reservation as to the rank of the allopatric *T. pangani* and *T. girigan* relative to each other. *T. jipe* though superficially like *T. girigan* has very distinctive pharyngeal teeth quite unlike *T. mossambica* and more like *T. galilaea* (Linn.). Further knowledge of the ecology of all these species is required before the interspecific relationships can be understood.

These Tilapia are, however, already being used on fish farms and transported round the countryside. It is therefore very desirable that those responsible for the fish should be able to name them to record movements, quite apart from the desirability of recording as much as possible about natural distribution before species from different river systems are inevitably mixed. For example, further study has shown that fish of supposed "*T. nilotica*" grown in the Tanganyika Government's experimental fish farm at Korogwe really belong to the new species *T. pangani*, and appear to be more nearly related to *T. mossambica* than *T. nilotica ;* this explains the differences in behaviour between these fish and the genuine *T. nilotica* which have been tried in dams in Uganda and the Belgian Congo.

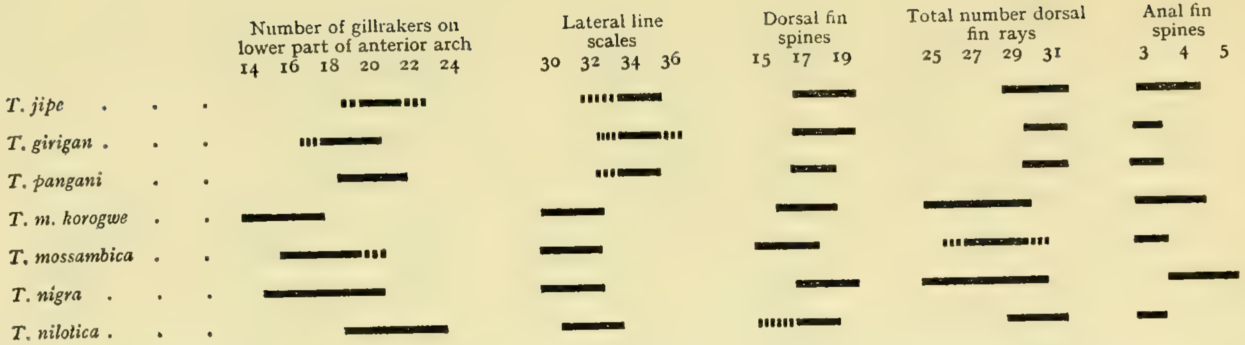
The situation has been further complicated by the introduction of four distinct species foreign to the Pangani system into the Korogwe ponds, *T. esculenta* Graham and *T. variabilis* Blgr. from Lake Victoria, and T. *macrochir* Blgr. and *T. melanopleura* A. Dum., from the Belgian Congo. There are also reports that *T. nigra* Günther was once introduced into streams flowing south from Kilimanjaro, streams which also find their way into the Pangani.

T. mossambica korogwe which was not intentionally stocked in the Korogwe ponds was nevertheless found in them and presumably gained access from the Pangani water supply together with some small *Haplochromis* which also appeared in these ponds. These accidental entries into ponds indicate the difficulty of making really fishproof screens and the need to examine the indigenous Tilapias in these rivers before escapes from ponds, and possibly hybridization with the local species, occur.

A summary of the diagnostic characters of the new forms is given in Table I, and some of their characters are compared with those of *T. mossambica*, *T. nigra* and *T. nilotica* in Text-fig. 2.

TABLE I.—*Diagnostic characters of new species of Tilapia*

		T. jipe sp.n.	*T. girigan* sp.n.	*T. pangani* sp.n.	*T. m. korogwe* sub. sp.n.
No. on which detailed measurements made: Size range—total length cm.		12 of 12–27	19 of 16–31	8 of 22–29	12 of 11–18
$\frac{\text{Body depth}}{\text{Standard body length}} \times 100$		36·0–40·2	34·2–40·4	31·7–43·5	35·2–40·7
$\frac{\text{Head length}}{\text{Standard body length}} \times 100$		32·0–36·2	31·6–36·2	30·8–34·3	32·3–35·7
$\frac{\text{Pectoral fin length}}{\text{Standard body length}} \times 100$		35·2–42·2	30·0–37·4	31·7–39·9	—
$\frac{\text{Lower jaw}}{\text{Head length}} \times 100$		25·8–33·8	27·8–38·6	32·2–37·1	(34·4 ♀) 36·1–44·5 ♂
$\frac{\text{Snout}}{\text{Head length}} \times 100$		29·7–39·7	31·9–42·7	34·9–40·4	(34·4 ♀) 36·6–40·0 ♂
$\frac{\text{Interorbital width}}{\text{Head length}} \times 100$		33·3–40·0	34·4–38·9	34·2–38·2	31·0–36·0
$\frac{\text{Preorbital depth}}{\text{Head length}} \times 100$		18·7–22·4	18·1–21·7	21·4–23·3	19·05–22·5
Caudal peduncle $\frac{\text{length}}{\text{depth}}$		0·80–1·05	0·79–1·00	0·8–1·0	0·69–0·95
Lower pharyngeal bone	$\frac{\text{length}}{\text{width}}$	0·95–1·22	0·81–1·00	0·97–1·08	0·91–1·01
	toothed area	Heart-shaped	Large triangular	Smaller triangular	—
	teeth	Fine, densely crowded	Coarse, well scattered	Intermediate	—
Teeth: number of series	upper jaw	5–8	4–8	5–8	4–5
	lower jaw	5–7 (8)	4–6	4–6	4–5
Number of gillrakers on lower part of anterior arch		(19) 20–21 (22)	(17) 18–20	19–21	14–17
Dorsal fin	Number of spines Number of soft rays	17–19 11–13 } 29–31	17–19 12–14 } 30–31	17–18 12–13 } 30–31	16–18 9–11 } 25–29
Anal fin	Number of spines Number of soft rays	4 or 3 10–12 } 14–16	3 11–13 } 14–16	3 11–13 } 14–16	3–4 8–11 } 11–14
Scales	Lateral line series	(32) 34–35	(33) 34–35 (36)	(33) 34–35	30–32
	Around caudal peduncle	17–20	17–20	18–20	16–17 (18)
	Number of series (below eye) on cheek	2	2–3	3	2–3



TEXT FIG. 2.—A comparison of various characters of the newly described species with those of samples of *T. mossambica* Peters (Zambesi and southwards), *T. nigra* Gthr. (R. Athi) and *T. nilotica* L. (R. Nile). Less frequent parts of ranges shown by broken lines.

II. SYSTEMATIC DIAGNOSES

Tilapia jipe sp. n.

(Pl. 13 and 16A)

16 specimens of 5–20 cm. total length from Lake Jipe.

54 specimens of 7–28 cm. from ponds stocked from Lake Jipe.

Tilapia with body proportions, teeth, fin rays, scales and gill-rakers as in the accompanying table of diagnostic characters (Table I). Lower pharyngeal bone with heart-shaped dentigerous area covered with dense velvet of fine teeth (Pl. 16A). Dorsal profile of head convex in smaller specimens but jaws become elongated in mature males giving a concave upper profile. Fin rays long, pectoral generally reaching origin of anal and posterior tip of dorsal extending halfway along caudal; caudal fin long with very definite vertical black or dark brown stripes.

Non-breeding fish light grey with spotted effect caused by the very distinct black or dark brown centre to each scale along back and sides, belly light grey. Faint indications of 7–9 darker vertical stripes on body of some specimens; dorsal and anal fins grey, spotted anteriorly and striped posteriorly with black; caudal fins with vertical stripes; pectoral fins unpigmented, pelvics becoming dark in larger fish. Breeding fish, particularly males, develop green and purple sheen, bright orange edge to dorsal fin and crimson edge to caudal, bluish-green pelvics and bluish-green edge to anal in some specimens; no genital tassel. Fry up to about 8 cm. long have olive-greenish body with 10–14 thin vertical dark brown stripes stretching from dorsal to ventral surface, caudal and hind end of anal striped as in adults; well marked black "*Tilapia* mark" on a clear background extending from the last dorsal spine to the third or fourth soft ray, and followed by three definite black bars on hind end of dorsal fin.

Among the 70 *T. jipe* preserved, 12 (17%) had three anal spines, 5 (7%) had three plus a partly ossified fourth, 52 (75%) had four and 1 (1%) had five.

The type is a male of 162 + 45 mm. (British Museum (Natural History) register number 1952.2.26.2) and the allotype is a female of 140 + 35 mm. (B.M.(N.H.), 1952.2.26.1), both collected from Lake Jipe in January, 1951.

The striped tail (previously thought to be characteristic of *T. nilotica* in East Africa) and general appearance of *T. jipe* are similar to *T. nilotica* Linn., but in contrast with this species, *T. jipe* generally has 4 anal spines and a shallower body, smaller head, wider interorbital, more rows of teeth in the jaws, and the jaws of mature males become accentuated, a characteristic of the *mossambica* group of *Tilapia* and not shown by *T. nilotica*. The pharyngeal bone of *T. jipe* is quite distinct and characteristic, the dense velvet of fine pharyngeal teeth being most like that of *T. galilaea* (L.); however, *T. jipe* differs from *T. galilaea* in having a shallower body, a longer snout accentuated in mature males, a less deep preorbital bone, more lateral line scales, and usually four anal spines.

T. jipe is easily distinguished from the sympatric *T. girigan* by the striped caudal fin, four anal spines, pectoral fin reaching origin of anal fin, the heart-shaped dentigerous area and fine teeth on the lower pharyngeal bone, less concave profile, and lighter body colour with very distinct spots.

T. girigan sp.n.
(Pl. 14 and 16B)

22 specimens of 5–31·5 cm. total length from Lake Jipe.

9 specimens of 7–23 cm. total length from ponds stocked from Lake Jipe.

Tilapia with body proportions, teeth, fin rays, scales and gill-rakers as shown in the diagnostic Table I. Lower pharyngeal bone with large triangular toothed area and straight posterior edge; pharyngeal teeth coarse and well scattered on bone (Pl. 16B). Jaws becoming elongated in mature fish, more markedly in the males, giving concave upper profile. Fin rays not very long, pectoral not reaching origin of anal; caudal fin immaculate or uniformly dark, or with spots and blotches, but not striped.

Non-breeding fish dark olive-brown, spotted effect due to black or dark brown centre to all the scales on back and sides extending right down to the grey ventral surface. Indications of about nine vertical black or dark brown stripes on some specimens. Dorsal and anal fins dark grey with posterior ends spotted or blotched with black; pectorals immaculate; pelvics dark grey. Breeding males with red or orange margin to dorsal and caudal fins; no genital tassel. Fry up to about 8 cm. total length olive-brown with 10–14 vertical dark stripes; " *Tilapia* mark " as in *T. jipe* fry, but general body colour darker and caudal and hind end of dorsal immaculate or spotted as in adults, but not striped as in *T. jipe* fry.

The type is a male of 210 + 49 mm. (British Museum (Natural History) register number 1952.2.26.3), and the allotype is a female of 177 + 45 mm. (B.M.(N.H.), 1952.2.26.4), both collected from Lake Jipe in January, 1951.

In general body shape and in the development of the jaws and the concave profile of the mature males *T. girigan* resembles *T. mossambica* Peters. It differs from *T. mossambica,* however, in having a higher number of dorsal and anal fin rays [30–31 dorsal rays instead of (26) 27–29 (30), and 14–16 anal rays instead of 12–15], more scales in the lateral line series (33–36) instead of 30–32 in *T. mossambica*), more gillrakers [(17) 18–20 in contrast to 16–19 (20)], and the outer teeth in the jaws remain bicuspid, whereas they often become unicuspid in mature male *T. mossambica.* Also the lower pharyngeal bone of *T. girigan* has a shorter blade and stouter appearance than in *T. mossambica* (compare Pl. 16. B and E.). The pharyngeal teeth of *T. girigan* are most like *T. nilotica* Linn., (Pl. 16F) but the toothed area is larger in *T. girigan. T. girigan* has a higher number of scales in the lateral line series (33–36 instead of 31–33 in *T. nilotica*), and lacks the striped tail of *T. nilotica.* Males of *T. girigan* show lengthening of the jaws and development of a concave profile as in *T. mossambica,* a character not found in *T. nilotica. T. girigan* is very like *T. pangani* and may have arisen as a lake form of this species, but in *T. girigan* the lower pharyngeal bone and the toothed area are larger and the teeth considerably coarser, longer, stronger and more scattered on the bone than in *T. pangani* of comparable sizes, and the preorbital bone is not so deep. *T. girigan* from Lake Jipe were considerably darker in colour than *T. jipe* from the lake, and darker and more spotted than *T. pangani* ; in both *T. girigan* and *T. jipe* specimens from the ponds were lighter in colour and more spotted than those from the lake.

T. pangani sp. n.

(Pl. 15 and 16c).

8 specimens of 22–29 cm. total length.

Tilapia with body proportions, teeth, fin rays, scales and gillrakers as shown in the diagnostic Table I. Lower pharyngeal bone smaller and with smaller toothed area, and with a flatter posterior edge than that of *T. girigan ;* pharyngeal teeth finer, particularly anteriorly, and closer together than in *T. girigan*, but coarser than in *T. jipe* (compare Pl. 16c with A and B). Jaws lengthening in mature males, giving concave upper profile. Dorsal, anal and caudal fin rays as long as in *T. girigan*; pectoral not reaching origin of anal; caudal fin with dark spots or blotches, or slight stripes at base only (not striped as in *T. jipe*).

Non-breeding fish brownish or grey, dark centres to scales on body but general impression not so spotted as in *T. girigan* or *T. jipe*; indications of vertical stripes (about 9) in some specimens; pectoral fins, and in some small ones pelvics, immaculate; pelvics pigmented in larger specimens. Posterior end of dorsal and anal fins spotted or barred with dark brown or dark grey. Breeding fish, particularly males, lose the vertical stripes, develop a purple-green sheen, dark pelvic fins, bright orange margin to dorsal and bright crimson margin to caudal fin ; no genital tassel.

The type is a male of 236 + 74 mm. collected from the Pangani River near Korogwe by Major Gould in 1949 [British Museum (Natural History), register number 1952.2. 26.39], and the allotype is a female of 189+46 mm. collected from a Korogwe fishpond, stocked from the Pangani River, in January, 1951 [B.M.(N.H.), 1952. 2.26.40].

T. pangani is like *T. mossambica* Peters in general facies and development of the jaws and concave profile of the mature male, but in contrast with *T. mossambica* it has (*a*) a higher number of dorsal fin rays [30–31 ; contrast (26) 27–29 (30)] ; (*b*) a higher number of anal rays (14–16 contrast ; 12–15) ; (*c*) more scales in the lateral line series [(33) 34–35 ; contrast 30–32]. *T. pangani* is distinguishable from *T. girigan* by the more *mossambica*-like pharyngeal teeth on the smaller lower pharyngeal bone, and the deeper preorbital bone.

It is interesting to note here a report from Major Gould that whereas *T. mossambica* from the lower Pangani can be transferred to, and live in, seawater lagoons, *T. pangani* does not survive this transfer.

T. mossambica korogwe subsp. n.

(Pl. 16D).

12 specimens of 11–18 cm. total length.

Tilapia with body proportions, teeth, fin rays, scales and gillrakers as shown in the diagnostic Table I. Lower pharyngeal bone with short blade, toothed area very like *T. mossambica* but teeth slightly coarser. Mouth very large, wide and thick-lipped with wide tooth bands; jaw teeth small, poorly developed, weakly cuspidate and well embedded, teeth of both outer and inner series tending to be unicuspid at the sides of the mouth in almost all specimens (including the female). Eyes much more dorso-lateral than in other *Tilapia*. Pectoral fins short, not reaching anus.

Body dark silvery grey, longitudinal black bands along lower lateral line, with indications of about 7 vertical black bars across this line. Line of 4 or 5 black spots above dorsal lateral line and black spot on dorsal side of caudal peduncle. "*Tilapia* mark" an oval black spot near hind end of dorsal fin. Tail immaculate dark grey. Long dorsal and anal fins ; anal and pelvics and ventral surface of body dark grey. Mature males with white or grey tip to caudal fin and small (2 mm.) white genital papilla. Female (one specimen only) lighter grey with more definite vertical black stripes (8) and black spot on dorsal side of caudal peduncle ; mouth not so large as in males.

This *Tilapia* appeared in several of the fishponds at the Tanganyika Government experimental fish farm at Korogwe. Its origin is uncertain but it seems most probable that it gained access to the ponds with the water supply, which is a cut flowing from, and returning to, the Pangani River. Only one female, caught together with the males and believed to be the female of this subspecies, was found, so the description of the female given above must be considered with reservation.

The type is a male of 140 + 43 mm. collected by Gould in 1951, from one of the Korogwe ponds [British Museum (Natural History) register number 1952.2.26.37]. The one female of 91 + 29 mm. collected in January, 1951, from one of the Korogwe ponds [B.M.(N.H.), 1952.2.26.5] is considered, on present evidence, to be the female of this subspecies and is, therefore, selected as the allotype.

T. mossambica korogwe is very like *T. m. mossambica* in general facies and in the development of the concave upper profile in the males and in the simplification of the jaw teeth, but it has a lower number of gillrakers [14–17 instead of 16–19 (20) in *T. mossambica*], a higher number of dorsal spines (16–18; contrast 15–17 in *T. mossambica*), and four anal spines in some specimens.

In *T. mossambica korogwe* the lower pharyngeal bone has a slightly shorter blade and the pharyngeal teeth are slightly coarser than in *T. mossambica*. The head and mouth are wider in *T. mossambica korogwe* and the simplification of the jaw teeth is even more marked than in *T. mossambica* of comparable sizes and extends to the inner series of teeth. *T. mossambica korogwe* is easily distinguished from *T. jipe*, *T. girigan*, *T. pangani*, *T. nilotica* and *T. esculenta* by the following characters : the very wide head, wide mouth and wide lips, relatively narrow interorbital and the dorso-lateral eyes, small eyes, large preorbital, elongated very concave snout, pelvics far forward and pelvic-anus distance long.

OTHER *TILAPIA* FROM THE PANGANI RIVER

The British Museum collection contains three other specimens of *Tilapia* from the Pangani River and certain fry collected from the Korogwe fish ponds which do not seem to belong to *T. pangani*, *T. mossambica korogwe* or any of the *Tilapia* species stocked in the ponds. Two of these specimens were collected by Gould in 1949 from the Pangani River together with *T. pangani;* the male was much darker than *T. pangani*, less spotted and with indications of 7 vertical dark bars. These two fishes differed from *T. pangani* in having (*a*) 4 anal spines and 10 soft rays, (*b*) 17–18 dorsal spines and 10 soft rays, (*c*) 31 scales in the lateral line series (instead of 33–35), (*d*) 15–16 gillrakers on the lower part of the anterior arch (contrast 19–21 in *T. pangani*). In all these characters they correspond well with *T. nigra* Gthr. There are reports that *T. nigra* were once introduced into the streams flowing from the south side of Kilimanjaro ; such streams drain into the Pangani, so these fishes may not be indigenous. Two small *Tilapia* (7–8 cm.) found in the Korogwe ponds stocked with *Tilapia* from the Taveta ponds also appear to be *T. nigra*, and may have entered this pond with the water supply from the Pangani.

The British Museum collection also contains a 17 cm. *Tilapia* with three anal spines, 33 scales in the lateral line series and 20 gill rakers, collected from the Pangani by Playfair in 1865, and identified as *Chromis niloticus*[1] (= *T. nilotica*). This fish does not appear to belong to any of the other species described from the Pangani system. *Chromis niloticus* (Hasselquist) collected from the Ruvu (Pangani) at Korogwe are also described by Pfeffer (1896), but the number of specimens seen is not stated. Boulenger (1915) assigns the *C. niloticus* described by Pfeffer to *Tilapia natalensis* (Peters) and *T. nilotica* L. The illustration given by Pfeffer shows that in general facies his *C. niloticus* differs considerably from *T. nilotica* from the type locality, although it agrees with *T. nilotica* in many characters such as the numbers of lateral line scales and gillrakers. No other specimens like Playfair's fish have been found in recent collections; until further material is forthcoming it is impossible to say how this and Pfeffer's fishes relate to the other Tilapias.

III. FIELD AND POND OBSERVATION

A. *T. girigan* and *T. jipe* in Lake Jipe and ponds.

Prior to these investigations it was presumed that the *Tilapia* population in Lake Jipe consisted of one or possibly two new species related to *T. mossambica*. No specific name had yet been given to these fish which were merely referred to as Lake Jipe Tilapia. Field observations did not reveal for certain the existence of two species, but it was noticed that some fishes had four and some had three anal spines, and that the four-spined fishes had a striped caudal fin whereas in the three-spined the caudal fin was striped, spotted or immaculate.

Subsequent examination of samples kept for laboratory study showed that all the four-spined Tilapia belonged to the species now called *T. jipe*, whereas the three-spined Tilapia included both *T. jipe* and *T. girigan*, in the proportion 1.12 *T. jipe*: 1.00 *T. girigan*. The proportions of the two species in the preserved samples suggested that most of the *Tilapia* seen from Lake Jipe happened to be *T. girigan*, whereas most of those from the ponds were *T. jipe*. Many more *T. jipe* than *T. girigan* were found among the fry used for stocking the ponds, which helps to explain the predominance of *T. jipe* in the ponds ; these fry, 2–10 cm. long, were caught by pulling a sack-cloth seine to the shore through a clearing in the reeds bordering Lake Jipe. Whether *T. girigan* fry inhabit a different zone in the lake or would be found in greater numbers at other times of the year is not known. The large *Tilapia* from Lake Jipe, among which *T. girigan* predominated, were caught by beating the water around gillnets set by day among the patches of water weed.[1]

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[1] Playfair & Günther, 1896, page 111.

Twenty-two Lake Jipe *Tilapia* were taken from Taveta to Korogwe Ponds, sixteen had four anal spines and were probably *T. jipe*, three had three anal spines and may have included *T. girigan*, and three had a partly ossified fourth spine. Two of these *Tilapia* were presented to the British Museum in December, 1951, and identified as *T. jipe ;* this confirms the presence of this species at Korogwe. The presence of *T. girigan* at Korogwe needs confirmation ; a sample of fry from Korogwe ponds indicates that *T. girigan* were also there, but *T. girigan* fry are difficult to distinguish from *T. pangani* fry which might have found their way into the ponds accidentally with the water supply.

Length frequencies of male and female *T. jipe* and *T. girigan* are given in Text-fig. 3A and B and summarized in Table II.

TABLE II.—*The sex ratio, length range and minimum breeding sizes of* T. girigan *and* T. jipe.

Place	Fishing method	Species	Sex ratio		Body length (cm.)		Minimum breeding size	
			Male	Female	Male	Female	Male	Female
L. Jipe	Gillnet	Mainly *T. girigan*	41	26	16–32	16–32	21	17
Taveta pond	Pond emptied	*T. girigan* and *T. jipe* (3 anal spines)	143	15	14–28	15–22	21	18
		T. jipe (4 anal spines)	216	36	15–25	14–21	21	15
Taveta pond	Angle	Mainly *T. jipe*	12	4	17–27	15–17	—	—
Korogwe pond	Pond emptied	*T. jipe* and ? *T. girigan*	24	14	23–30	16–23	—	—

It is immediately clear that in both lake and pond samples, and in those in which *T. girigan* or *T. jipe* predominated :

(*a*) the males were considerably larger than the females ;
(*b*) females started to spawn at a smaller size than the males ;
(*c*) the sex ratio was very unequal, males being more numerous than females ;
(*d*) the pond reared fish were of comparable lengths and minimum breeding sizes with the fish from the lake.

The length/weight relations of *T. girigan* and *T. jipe* are indicated in Text-fig. 4. The pond-reared fish were in very poor condition, i.e. showed a low weight for length, compared with the *Tilapia* from Lake Jipe. This was evidently the result of lack of food in the ponds.

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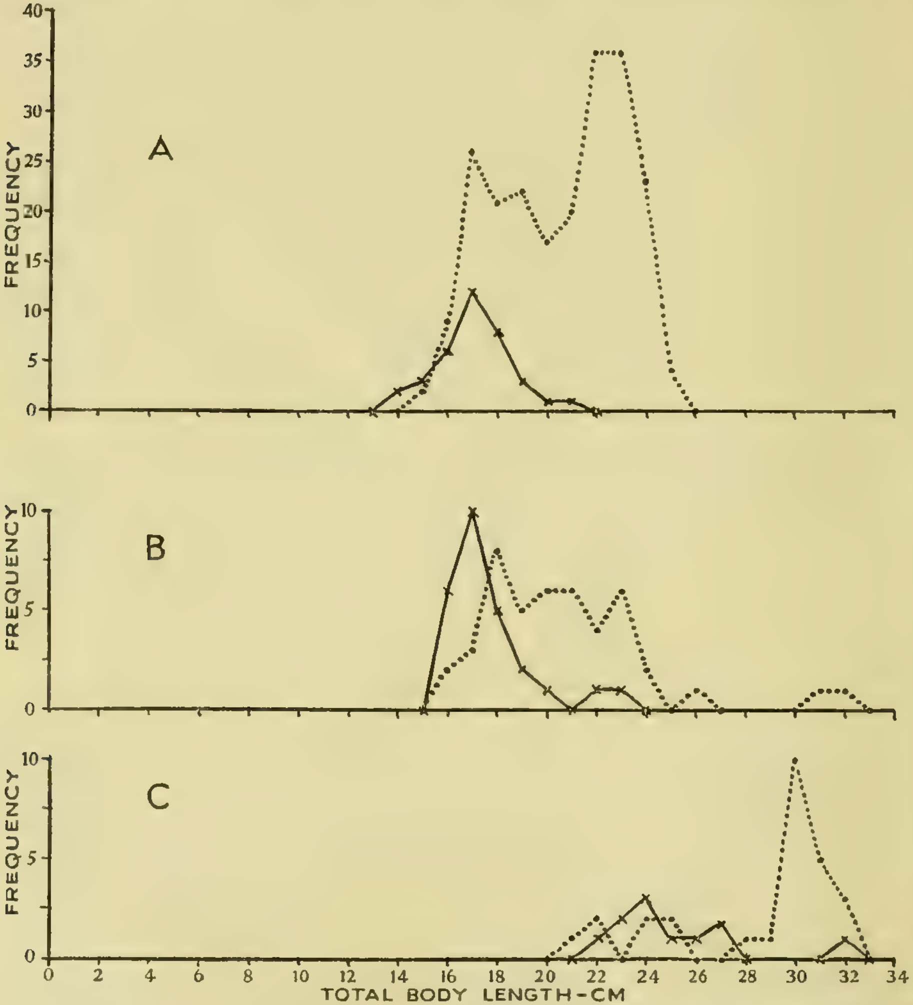
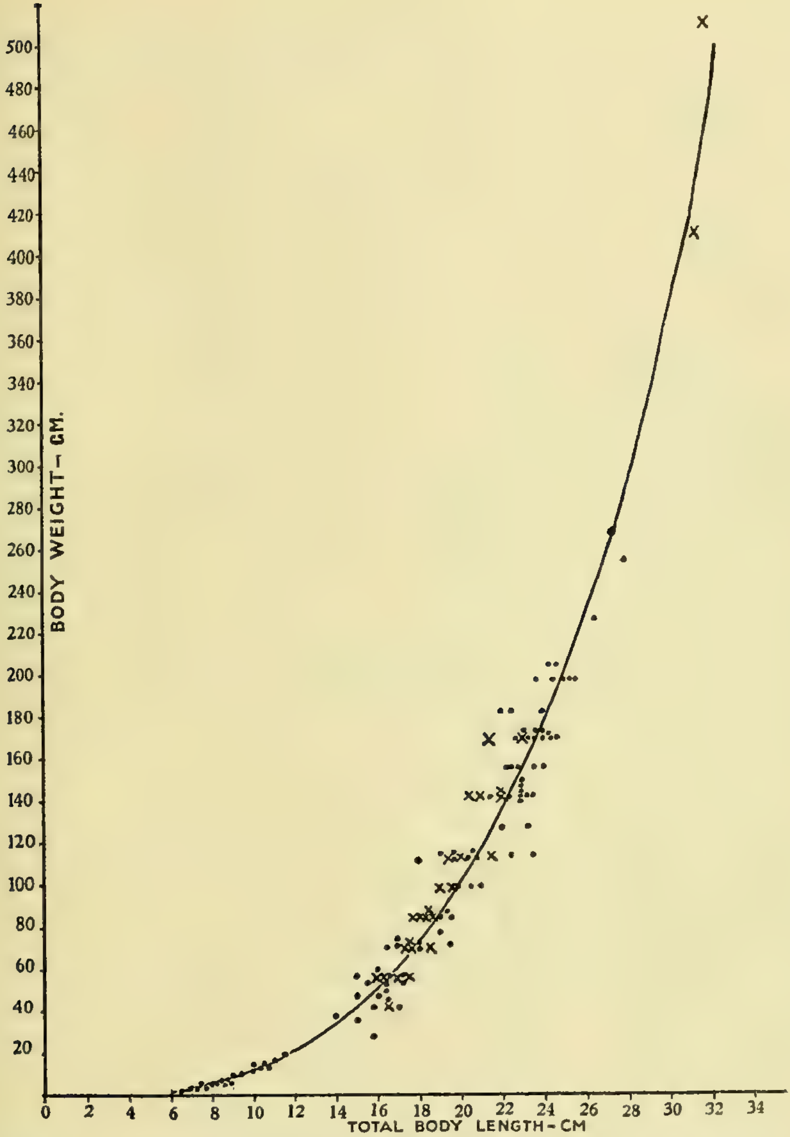
[1] *Petersius tangensis* Lonnberg, previously recorded from Tanga, and *Barbus paludinosus* Peters, a species widely distributed in East Africa, were also caught in Lake Jipe. These species grow only to about 10 cm. long. A few *Clarias mossambicus* Peters, another species widely distributed in East Africa, were found when the Taveta pond was emptied.

The Taveta pond which was emptied on 16th January, 1951, was said to have been stocked with 4–8 cm. *Tilapia* from Lake Jipe about fifteen months previously. After fifteen months in the pond the *T. jipe* (i.e. those *Tilapia* with four anal spines) males were 15–25 cm. long (about 40–200 gm.) with pronounced modes at 17 cm.



Text-fig. 3. Length frequencies of Lake Jipe and Pangani River *Tilapia* reared in fishponds. Males ...., females ————. A. Tilapia with four anal spines, probably all *T. jipe*, examined when a Taveta pond was emptied fifteen months after stocking with 2–10 cm. fish from Lake Jipe. B. Tilapia from Lake Jipe mainly *T. girigan*. C. *T. pangani* from a Korogwe pond.



TEXT-FIG. 4. The length/weight relationship of Lake Jipe *Tilapia*. Data from 27 *Tilapia* from Lake Jipe, mainly *T. girigan*, marked thus × ; all other *Tilapia* from Taveta fishponds and mainly *T. jipe*. (Curve fitted by eye.)

and 22–23 cm., and females were 14–21 cm. (about 30–120 gm.), with a pronounced mode at 17 cm. (Text. fig. 3A). Among the three-anal-spined *Tilapia* (T. *girigan* and *T. jipe*) from the pond the males were 14–28 cm. (30–206 gm.) and females 15–22 cm. (40–140 gm.). Both species had been breeding for some time as the pond contained numerous fry of 6–11 cm.; *T. jipe* fry were the more numerous but fry of both species were found.

Adult *Tilapia* from Taveta ponds were taken to Korogwe in October, 1950, and numerous fry 2–6 cm. long of *T. jipe* and probably also *T. girigan* (see above) were seen when the pond was examined in January, 1951.

Text-fig 3B gives the relative sizes of males and females from catches in Lake Jipe in which *T. girigan* were highly predominant. Both *T. girigan* and *T. jipe* females were breeding at a considerably smaller size than the males. In Lake Jipe *T. girigan* males of 21 cm. (about 140 gm.) and females of 17 cm. (about 60 gm.) were spawning. In the Taveta pond *T. jipe* males were also spawning at 21 cm. (though only about 120 gm. weight), and females of 15–21 cm. (about 28–120 gm.) were ripe. The ovaries of ripe *T. jipe* from the Taveta pond were dark yellow and counts of ripe eggs in the ovaries showed that 200–250 eggs are laid at a time by these small females. *T. jipe* females are oral incubators; females were found with up to 167 eggs in the mouth and others were seen carrying yolked young. In the Taveta pond females as small as 15 cm. long were found brooding eggs. *T. girigan* is also a mouth brooder ; up to 60 eggs were found in the mouth of one female. No males of either species were found carrying eggs.

Although no *Tilapia* nests were seen on the bottom of the Taveta pond, some were examined when the Korogwe pond stocked with Lake Jipe *Tilapia* was emptied. These nests (Pl. 17A) were identical in appearance with those made by *T. pangani*. Each nest consisted of two or three series of small pits around a larger central pit, the whole excavation being about two and-a-quarter feet across. It is not yet known for certain which of the two Lake Jipe Tilapias made this nest, but they were probably made by *T. jipe*, and similar nests have been reported from the Taveta ponds in which *T. jipe* predominated. It was surprising to find similar nests made by *T. jipe* (or *T. girigan*) and *T. pangani* and this observation needs confirmation by a more reliable correlation between nest and species responsible for it. For comparison with these nests Plate 17B shows the simple circular hollows, about twelve inches in diameter, made by *T. esculenta* in one of the Korogwe ponds.

The scales of 25 pond-living *Tilapia* showed that in most (88%) cases the immature fishes have uniform scales whereas the scales of the mature show "checks" ; these checks were near the edge of the scales in fishes which had recently spawned. In males the checks appear as a band of circuli spaced more closely than on the rest of the scale. In the females the checks are clear spaces, as though several circuli had been eaten away ; it is thought that these represented spawning marks. Several of the females grown from fry in the Taveta pond showed three (and one showed four) such "spawning marks" after about fifteen months in the pond. Such checks should prove useful for comparison of the growth of mature *Tilapia* under different conditions.

The two species of Tilapia had not been distinguished when the samples of stomachs and intestines were collected from *Tilapia* from the Lake, and data from pond fish were influenced by the food available in the pond. Hence the data are not sufficient to show any difference in feeding habits between the two species. Among the preserved sample of *Tilapia* from Lake Jipe, however, ten *T. girigan* contained food, mostly chewed water weed (*Najas* sp.) with a good supply of epiphytic diatoms and other algae, or vegetable debris and algae from the bottom of the lake. The two *T. jipe* preserved from Lake Jipe did not provide any information on the food of this species under natural conditions ; the dense felt of pharyngeal teeth in this species suggests that these fish feed on very small particles, probably algae, possibly phytoplankton. The guts of ten other *Tilapia* from the lake, probably mostly *T. girigan*, contained the same kinds of vegetable matter as the preserved *T. girigan*. In several cases both plant material and bottom debris occurred in different parts of the alimentary tract of individual fish showing that the individual *Tilapia* varies its feeding habit. The pond fish, both species, had been eating bottom debris or mud with very little organic matter. The size of the particles of bottom debris, etc., in the guts of the pond fish did, however, reflect the degree of coarseness of the pharyngeal teeth, the stomach and intestines of *T. girigan* containing larger particles than did those of *T. jipe*, which has much more dense pharyngeal teeth. As the rectum of Lake Jipe *Tilapia* in many cases contained food which was originally very different from that in the stomach it was difficult to be certain how much of the food eaten was used. It was clear, however, that diatoms were digested, that some plant cell contents were extracted, but that much of the plant material eaten and the bluegreen and green algae (including filamentous greens) pass through these *Tilapia* unused.

Most of the *Tilapia* examined from Lake Jipe carried large numbers of nematodes in the pericardium. Some of the pond fish were similarly parasitised ; the apparently more numerous parasites in the lake fish may be related to the more numerous aquatic birds on the lake.

B. *T. pangani*

A sample of 39 *Tilapia* originally caught in traps in the Pangani River and living in one of the Korogwe breeding ponds was examined. The 27 males ranged from 21 to 32 cm. long with a pronounced mode at 30 cm. and the females from 22 to 32 cm. with a mode at 24 cm. (Text-fig. 3C). The size of these fish and the sex ratio in this sample may perhaps have been due to selective action by the trap in the river. This pond also contained numerous fry of 1–10 cm. long and the nest identical in appearance with that shown in Plate 17A. These adults had been in the ponds for two years ; it was said that they had not grown much during this time and that batches of young were found every six weeks throughout the year. The pond contained little food for these fish.

C. *T. mossambica korogwe*

Nothing is known of the habits of this small *Tilapia* found together with *T. variabilis* and *T. pangani* in various ponds at Korogwe. It seems most probable that it gained access to the ponds with the water supply from the Pangani River. The

T. m. korogwe were very docile, lying quietly on the bottom of the pond when the pond was emptied and in contrast with *T. variabilis* which leapt about the mud very actively in similar circumstances. Males as small as 16 cm. long were ripe though they did not have a marked breeding dress. Intestines contained insect remains and algal filaments. In spite of little food in the ponds these fish were in fairly good condition which suggests that the breeding size of this species in the natural environment may be similar to that in these ponds. The largest specimen seen was 18 cm. long. The only female seen (to eight males) was 12 cm. long and the ovary was already ripening.

D. Lake Chala Tilapia, *T. hunteri* Günther

Lake Chala, an isolated lake on the foothills of Kilimanjaro in the Pangani drainage area, was visited on 15th January, 1951. The *Tilapia* from this lake, *T. hunteri* Günther, are endemic and of particular interest since there is no apparent inflow or outflow to this deep, clear lake. Only immature *Tilapia* were caught. *T. hunteri* has been described as having four anal spines; of the twenty-one caught, however, only seven had four anal spines, the other fourteen had three. The shores of Lake Chala are rocky and shelve steeply into deep water. The immature *Tilapia* were in small shoals, each shoal of similar sized *Tilapia*, feeding on algae and debris off the bottom between the rocks near the shore ; large numbers of crabs [*Potamon* (*Potamonautes*) *platycentron* (Hilgendorf)] were also living among these rocks. *T. hunteri* may be distinguished from *T. pangani*, *T. girigan*, and *T. jipe* by the long shallow body (body depth 36 %of standard length in 21 cm. fish), long narrow caudal peduncle (length/depth 1·35 in 21 cm. fish) and a small narrow toothed area on the pharyngeal bone. *T. hunteri* appears to be endemic to Lake Chala ; its relationship with other *Tilapia* is not yet known.

IV. LAKE VICTORIA SPECIES OF TILAPIA GROWN IN PONDS

T. esculenta Graham and *T. variabilis* Boulenger have been introduced into the experimental ponds at Korogwe. These species are endemic to Lakes Victoria and Kyoga and do not occur naturally in the Pangani System, but data concerning their growth in these ponds are given here, as in several respects they behaved rather differently from the Pangani system Tilapia grown in the ponds. The fry (less than 20 mm. long) of both species were taken from the mouths of brooding female fish caught near Mwanza at the south end of Lake Victoria and were introduced into a small pond at Korogwe on 16th June, 1950. These fish were examined on 21st January, 1951, six and three-quarter months later, and the following observations were made.

T. esculenta Graham

There were 9 males and 7 females surviving. The males had grown to 16–17 cm. and were ripe, the females to 17–19 cm. and had spawned (Text-fig. 5A). The bottom of the pond had 46 nests, although only 16 breeding fish were present.

Each " nest " was a simple circular hollow in the bottom mud, about twelve inches across and a few inches deep (Pl. 17B); these nests were in about three feet of water.

Numerous *T. esculenta* fry up to 7 cm. total length were seen. It was said that this pond had been emptied and fry observed early in December, only six months after the original fry were put into the pond.

These *Tilapia* had very little nutritious food. Stomach contents showed that they had been feeding on bottom mud and diatoms. Many of the diatoms in the stomach were already empty or half empty and some diatoms in the rectum still contained some contents, possibly because of the amount of mud passing through the gut at the same time which might impede digestion.

In Lake Victoria male and female *T. esculenta* are generally at least 20–25 cm. long before they start to spawn. These *Tilapia* taken from the mouths of " normal sized " Lake Victoria *Tilapia* were breeding when 16–19 cm. long, and six and three-quarter months old.

T. variabilis Boulenger

There were 12 males and 13 females surviving. The males and females were growing at the same rate, fish of both sexes having grown to 13–19 cm. (with a mode at 16 cm). in six and three-quarter months (Text-fig. 5B). A number of the fish were ripe, but only one nest was seen. This was a simple circular hollow like the *T. esculenta* nests and like many of the *T. variabilis* nests seen in Lake Kyoga in Uganda.

Numerous fry 1–6 cm. long were present. It was said that no fry had been seen when the pond was emptied in December, 1950.

These *T. variabilis* were noticeably more active than the other *Tilapia* species, leaping about in the mud when the pond was emptied.

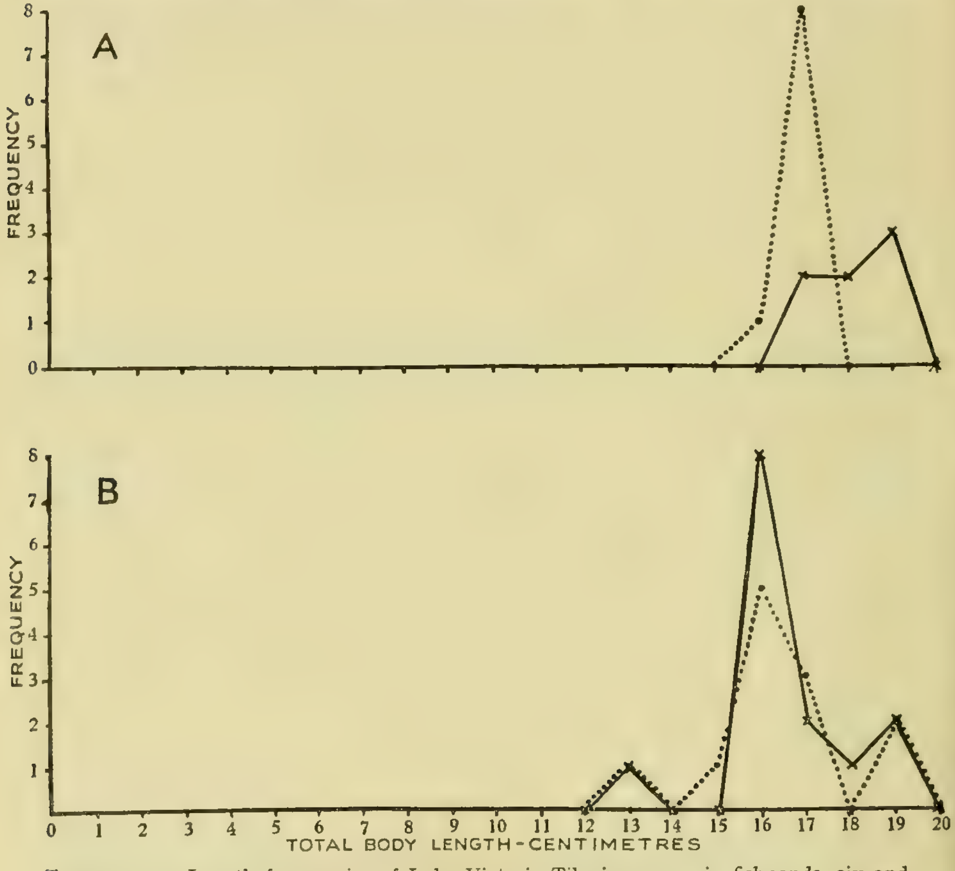
They had not grown quite so fast as the *T. esculenta.* Males and females showed the same rate of growth which bears out observations on Lake Victoria. Both sexes were breeding at 16 cm. long and when less then seven months old under these conditions, though in Lake Victoria from whence the fry came they would probably not start to breed until about 20 cm. long.

V DISCUSSION

The few odd specimens from the Pangani which do not fit into any of the new species described here suggest that there are further Tilapias in the Pangani system. Further field work is essential for sorting out these species and finding out how the various species keep distinct. Such field work needs to be done immediately as the introduction of species foreign to the Pangani system into ponds, and the probability that some will escape into the river, makes the task of unravelling species increasingly difficult and the results of less value in throwing light on the origin, evolution and distribution of these Tilapias.

It was expected that differences in breeding colours and nests would help to keep the species distinct, and it is surprising to find breeding colours so similar in the two species of Lake Jipe, and that the nests of these and of *T. pangani* should be alike. Further observations are required in the light of the definitions of the species here presented.

Among the *T. girigan* and *T. jipe* grown in the Taveta ponds the males were considerably larger than the females of the same age. Either the males grow faster than the females or they continue to grow after growth in the females has slowed down. It would be interesting to know how much this is an inherent character of these species and how much it may be influenced by the very unequal sex ratio, the more numerous males having more energy available for growth than the females who may be constantly engaged in reproduction. Among the *T. variabilis*, males and females grew at approximately the same rate, but there were approximately



TEXT-FIG. 5. Length frequencies of Lake Victoria Tilapias grown in fishponds, six and three-quarter months after the ponds were stocked with fry less than 20 mm. long. Males ....., Females ———. (A) *T. esculenta*. (B) *T. variabilis*.

equal numbers of males and females. Among *T. variabilis* and *T. esculenta* in Lake Victoria males and females are of comparable sizes and appear to grow at the same rate. The males of *T. mossambica* Peters are larger than the associated females, and Baerends and Baerends van Roon (1950) have shown that in this species[1] the size of the male is important in allowing him to establish and keep a spawning territory. Further observational and experimental work is needed to elucidate why sexual dimorphism and size differences exist in some species of *Tilapia* and not in others.

The snout of mature male *T. girigan*, *T. pangani*, and to a lesser extent *T. jipe* becomes elongated and the fish develops a very concave upper profile, as in *T. mossambica* Peters. The few large females also tended to develop the " male " profile, though to a lesser extent. Thus it seems that the elongation of the snout is partly a sexual character and partly a growth character, the snout showing positive allometric growth in relation to the growth of the fish.

This study has shown a variation in the number of anal spines in three species of *Tilapia*, *T. jipe*, *T. m. korogwe* and *T. hunteri* Günther ; this character was previously considered to be of considerable stability and specific significance in this genus. Trewavas (1937) described fossil *Tilapia* with four anal spines from Pleistocene deposits at Rawe near Lake Victoria and concluded that they belonged to *T. nigra* Günther. Greenwood (1951*b*) discussed fossil *Tilapia* with four anal spines from Miocene deposits on Rusinga Island, Lake Victoria, and considered these were most closely related to *T. mossambica* Peters, especially specimens from the Tana system (types of *Chromis spilurus* Günther 1894). Summarizing the geological evidence in connection with the distribution of *Haplochromis* species in East Africa, Greenwood (1951*a*) concluded that the eastward flowing rivers probably provided retreats for fish from Lake Karunga during the Miocene drying-up period. Lake Victoria now lies in part of the area formerly covered by Lake Karunga and it seems likely that the *Tilapia* found today in the Pangani system may have had a common origin with the four spined forms now fossilized near and in lake Victoria. Dr. E. Trewavas of the British Museum (Natural History) is at present studying the *Tilapia* of the Tana and other eastward-flowing rivers of East Africa. Her results are awaited with great interest and it is hoped that they will illuminate the relationships and probable lines of evolution of the species described here.

SUMMARY

Three new species and one new subspecies of *Tilapia* are described from the Pangani system, two species from Lake Jipe, *T. jipe* and *T. girigan*, and from the Pangani River a new species, *T. pangani*, and subspecies *T. mossambica korogwe*. *T. girigan* and *T. pangani* appear to be members of the *T. mossambica* complex. A few specimens do not fit into any of these species which suggests that there are further Tilapias in the Pangani. Further field work is necessary to see how the species keep distinct.

T. jipe has a vertically striped caudal fin, previously regarded as a specific "spot test " for *T. nilotica* Linn. in East Africa. The number of anal fin spines, a character

---

[1] *T. natalensis* = *T. mossambica* Peters (Trewavas 1937).

generally of specific significance among Tilapia, was found to vary in *T. jipe, T. m. korogwe* and *T. hunteri* Günther.

Length frequencies of lake and pond fish showed that in both *T. girigan* and *T. jipe :* (*a*) the males were considerably larger than the females ; (*b*) the females started to spawn at a smaller size than the males ; (*c*) males were much more numerous than females in the breeding population. " Nests " of Lake Jipe *Tilapia* and *T. pangani* are described and compared with the nests of *T. esculenta* Graham in neighbouring ponds.

Observations are given on the growth of *T. esculenta* Graham and *T. variabilis* Boulenger reared in ponds from fry from Lake Victoria. In both these species males and females showed the same rates of growth and started to breed at the same size. Both *T. esculenta* and *T. variabilis* in these ponds were breeding when 16 cm. long and less than seven months old, though in Lake Victoria, from whence the fry came, they would probably not start to breed until about 20 cm. long.

ACKNOWLEDGEMENTS

I would like to thank Colonel E. S. Grogan, and Major R. E. Gould, Fish Culturist in charge of the Korogwe Fish Farm, for their invaluable help while collecting the data on which this paper is based. I am very grateful to the Director of the East African Fisheries Research Organization and other members of the staff who have helped with stimulating discussion and criticism. To Dr. E. Trewavas of the British Museum (Natural History) my especial thanks are given for assistance and encouragement with the systematic side of the investigation. Plates 13–16 are the work of the staff of the photographic section of the British Museum (Natural History).

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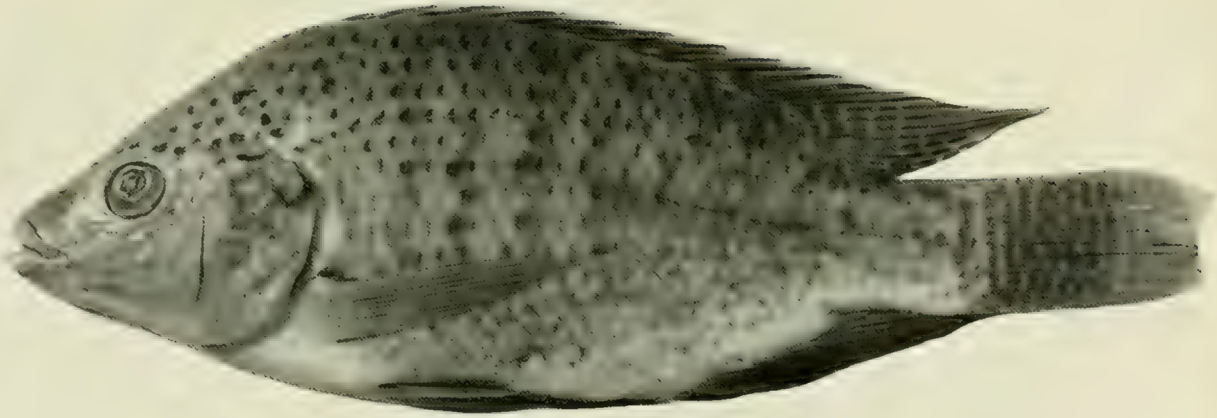
PLATE 13

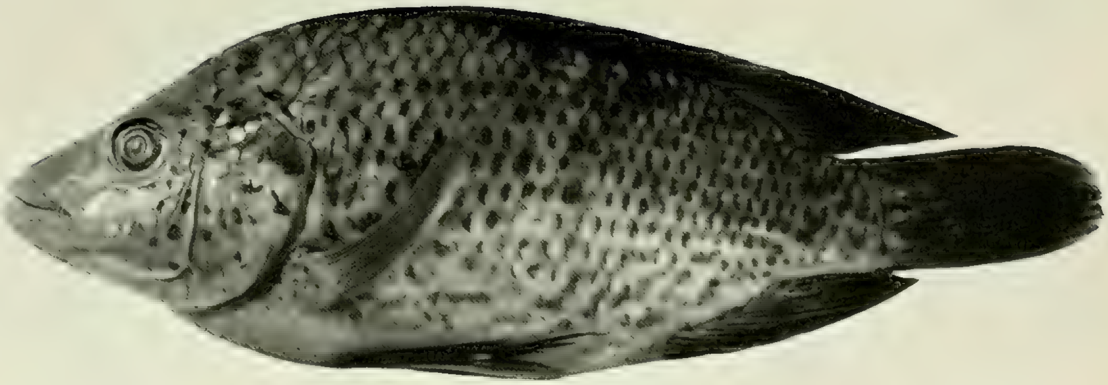
Tilapia jipe, a male of 25 cm. total length from one of the Taveta fishponds.



TILAPIA JIPE

PLATE 14

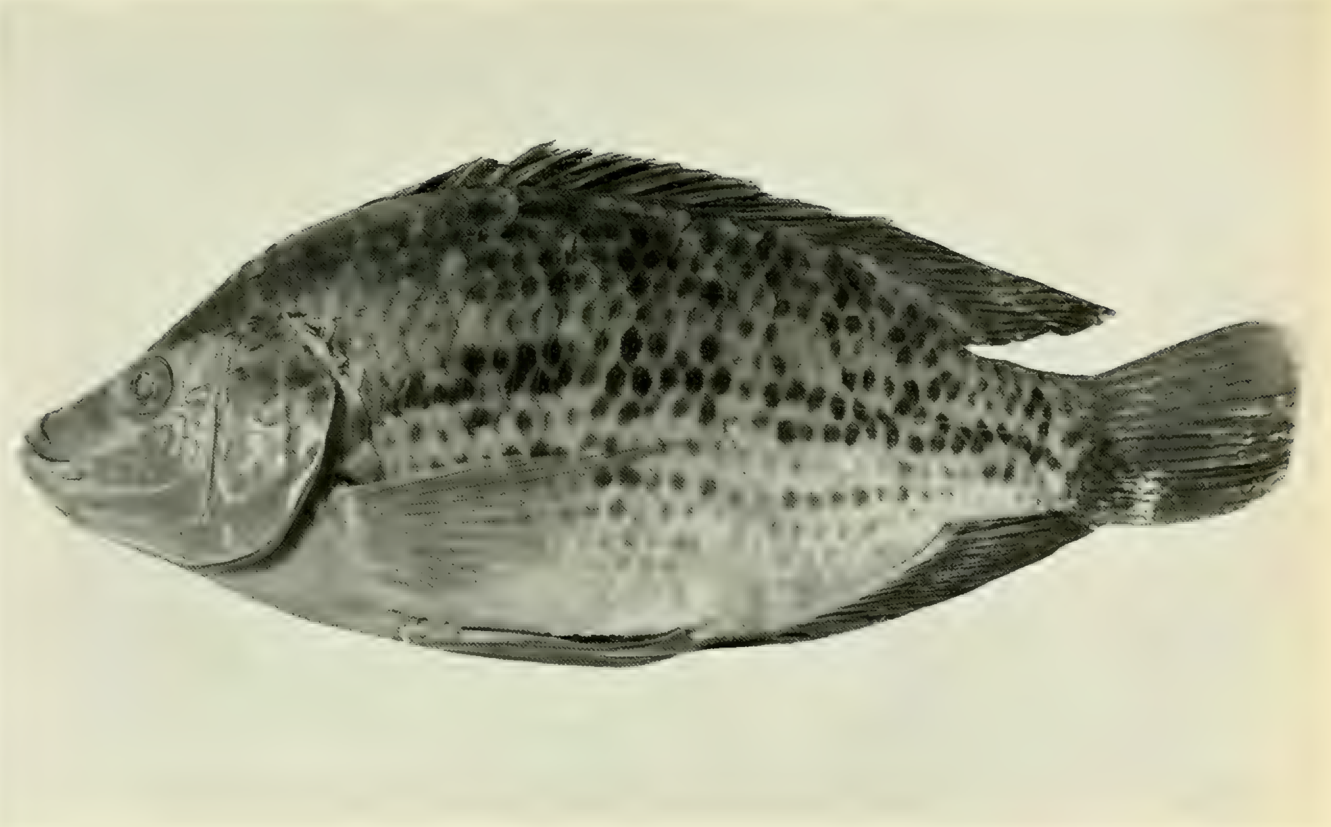
Tilapia girigan, a male of 23 cm. total length from Lake Jipe.



TILAPIA GIRIGAN

PLATE 15

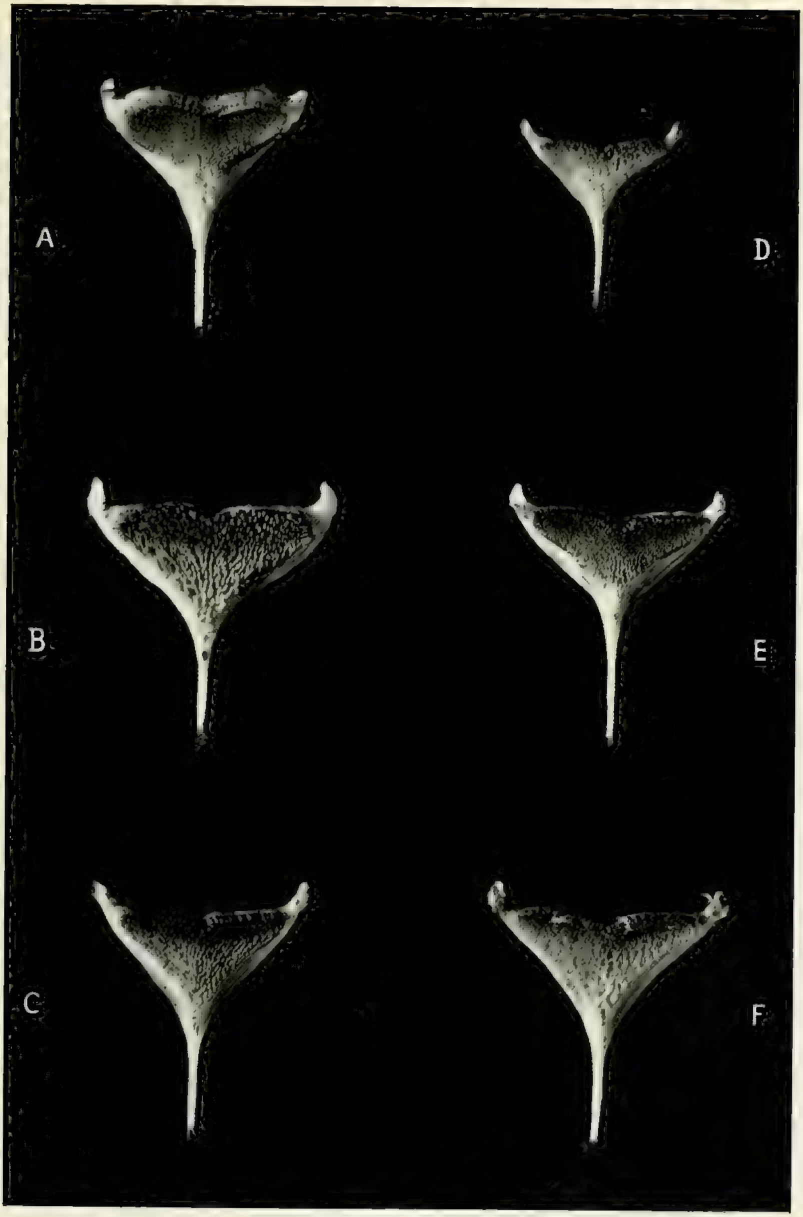
Tilapia pangani, a male of 28 cm. total length from one of the Korogwe fishponds.



TILAPIA PANGANI

PLATE 16

Lower pharyngeal bones of *Tilapia* species. A. *T. jipe* (fish 23 cm. total length). B. *T. girigan* (fish 23 cm.). C. *T. pangani* (fish 23 cm.). D. *T. mossambica korogwe* (fish 20 cm.). E. *T. mossambica* (fish 20 cm.). F. *T. nilotica* (fish 22 cm.)

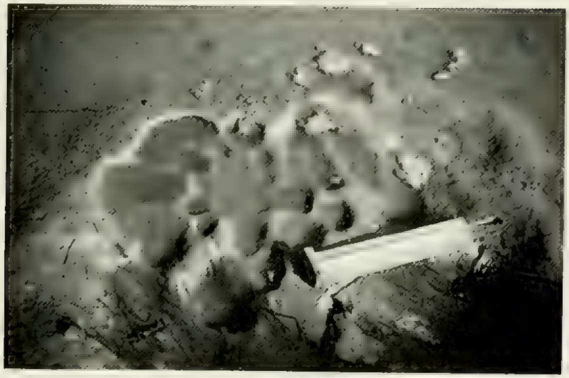


TILAPIA

PLATE 17

A. Nest of Lake Jipe *Tilapia* in one of the Korogwe ponds. The whole excavation is 2¼ft. across (the ruler is 15 in. long).

B. Nests of *Tilapia esculenta* from Lake Victoria in one of the Korogwe ponds. Each excavation is about 12 in. across.



TILAPIA

TILAPIA ESCULENTA

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THE MORPHOLOGY OF THE HEAD OF THE HAWFINCH

(COCCOTHRAUSTES COCCOTHRAUSTES)

-2 SEP 1955
PRESENTED

R. W. SIMS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 2 No. 13
LONDON: 1955

THE MORPHOLOGY OF THE HEAD OF THE HAWFINCH

(COCCOTHRAUSTES COCCOTHRAUSTES),

WITH SPECIAL REFERENCE TO THE MYOLOGY OF THE JAW

BY

REGINALD WILLIAM SIMS

*Pp.*369—393 ; 10 *Text-figures*

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THE MORPHOLOGY OF THE HEAD OF THE HAWFINCH

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SYNOPSIS

The ability of the Hawfinch, *Coccothraustes coccothraustes*, to crack open the stones of cherries, damsons and olives in order to feed on the kernels is generally well known, but the modifications which are present in the structure of the head and enable this comparatively small bird to perform such a feat have apparently received little attention. The method employed by *C. coccothraustes* to crack open the fruit stones is noteworthy because each stone is held between the mandibles and is broken solely by the force applied by the jaw muscles, and not by any " artifice " such as that employed by the thrush to smash snail shells, or the woodpecker to split almond stones. The behaviour of the bird when feeding on fruit stone kernels appears to follow a definite pattern. The bird usually selects fallen fruit apparently discarding the soft parts. Observations and photographs show that a cherry stone is positioned in the mouth by the combined movements of the head and tongue until it is held lengthways between the mandibles at the back of the horny palate of the mouth with the suture of the stone lying in the median sagittal plane of the head. A quick snap of the jaw and the shell is neatly cracked along the suture or " seam ". The halves of the shell are rejected and the kernel is swallowed whole, usually without being crushed. Experiments on breaking open cherry and olive stones (given in detail in the appendix) show that pressures in the region of about 100 lb. are required to perform this feat !

The purpose of this paper is to show how the head of *C. coccothraustes* is adapted to apply and withstand such forces by describing some aspects of the morphology of the head, namely, of the horny bill, or rhamphotheca, the skull and the jaw muscles.

MATERIALS

This study is based on specimens of *C. coccothraustes* collected in Great Britain. The material consists of two adults and two juvenile male specimens preserved in spirit in the National Collection, one head, sex unknown, supplied by Mr. G. R. Mountfort, and several skeletons in the National Collection. In most of the osteological material the rhamphothecae, which can only be removed with difficulty, were intact. The heads of two spirit specimens were dissected completely during the course of the investigation. The head of a spirit specimen of a Brambling, *Fringilla montifringilla*, was also dissected, and reference was made to the series of skulls of the Chaffinch, *Fringilla coelebs*, in the National Collection.

ACKNOWLEDGMENTS

I am indebted to Mr. Guy Mountfort for suggesting this investigation. The work was originally undertaken in order to answer some of the points raised by him in the preparation of his monograph of the Hawfinch. The scope of this study was subsequently enlarged. I am obliged to Mr. H. L. Cox and his colleagues of the National Physical Laboratory, and Mr. D. Welbourn of Cambridge, for providing me with the interesting data which form the appendix to this paper ; and to Dr. J. Wahrman of the Hebrew University, Jerusalem, for a supply of fresh olives for the crushing tests. I also wish to thank my colleagues in the British Museum (Natural History) for reading the MS. and for providing many helpful criticisms.

HISTORICAL NOTE

References to the general anatomy of the head of *C. coccothraustes* are remarkably few and are confined mainly to the consideration of characters of the skull as an aid to classification, or less frequently to its architecture. The skull with its high degree of ossification particularly impressed W. K. Parker (1879) by what he called " its ridgy strength " when he described some aspects of the anatomy of the skull in his systematic work on the structure of the palates of passerine birds. At the beginning of the section on *C. coccothraustes* he pointed out that most of the differences between the skull of this species and those of other members of the Fringillidae were of little phylogenetic importance because the modifications in the skull of *C. coccothraustes* were for " mechanical purposes". Nevertheless, Bowdler Sharpe (1888) used many of these modifications " for convenience " to separate what he termed the Coccothraustinae from the buntings and true finches.

The peculiarities of the horny bill or rhamphotheca were noted very briefly by Pycraft (1905), and his observations were occasionally referred to by subsequent workers. Nothing new was recorded on the horny bill until Sushkin (1925) described similar modifications in the bill of the Evening Grosbeak, *Hesperiphona vespertina*.

He concluded that they were essentially the same although purely adaptive characteristics. He agreed with W. K. Parker that most of the peculiarities of the skull were adaptive features, but believed that only one character of the bony palate was of systematic significance, and on that he regarded the Evening Grosbeak as a member of a sub-family containing the Old World hawfinches.

Later references are confined almost entirely to remarks in papers dealing with the mechanical structure of bird skulls, for example those by N. G. von Lebedinsky (1921) and von Kripp (1933*a*). The latter author showed that the skull was structurally stronger than that of a harrier.

The literature appears to contain few references to the myology of *C. coccothraustes*, so an account of the musculature of the jaw is given in this present paper. The nomenclature adopted is that proposed by Lakjer (1926) in his comparative work on the *Sauropsida*.

DESCRIPTION

1. *Rhamphotheca*

The rhamphotheca of birds is derived from the malpighian layer of the epidermis. In most birds it is seldom more than a thin sheath which is readily detached from a dried skull, but in *C. coccothraustes* parts of it inside the mouth are greatly thickened and enlarged. In the palatal region (Text-fig. 1*a*) it forms a longitudinally striated thick pad partly divided by a longitudinal median depression. This thickened area extends from the anterior border of the palatine bones over the posterior third of the premaxillae. The anterior two-thirds of the premaxillae are covered by the remainder of the horny palate which is strengthened by one median and a pair of lateral ridges. The grooves formed between the lateral ridges and the edges of the upper mandible accommodate the edges of the lower mandible. On the lower jaw (Text-fig. 1*b*) the horny sheath is thickened to form two large bosses which lie

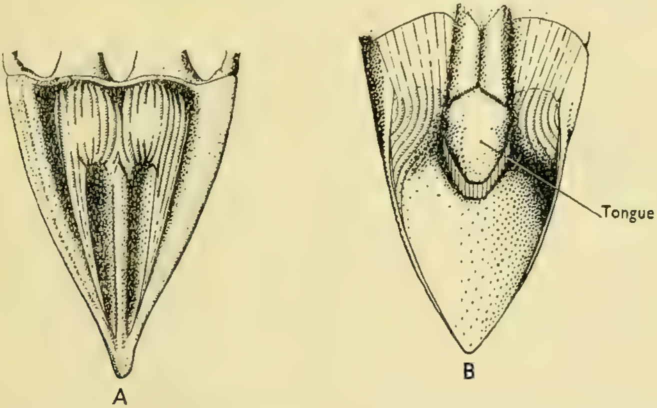

FIG. 1. ***Coccothraustes coccothraustes.*** The oral surfaces of the rhamphotheca showing the striated pads. A, Upper jaw; B, Lower jaw with the anterior of the tongue *in situ*.

immediately over the posterior parts of the dentary bones which are themselves specially thickened in this area. The bosses are striated, but the striations being curved more or less follow the contours. The depression between the two bosses accommodates the tongue. The tip of the tongue is broadly cuneiform in shape and lies flush with the anterior surfaces of the lateral bosses.

2. *Skull*

The principle modifications of the skull which appear to be connected with the ability of *C. coccothraustes* to exert a great force with its jaw muscles can be summarised as follows :

In the first place the whole skull is strengthened by a greater ossification than is usually found in most fringilline species. An indication of the extent of ossification as determined by weight, is given in a later section.

Von Kripp (1933*a*) described how the architecture of the skull is suited to withstand stress and strain. Viewed laterally the outline of the skull approximates to one horn of a crescent, the dorsal profile being convex and the central one concave (Text-fig. 2*a*). The concave ventral surface is strengthened by a system of struts formed by a massive pyterygoid-quadrate-zygoma system. The anterior part of the head is further strengthened by the heavily ossified nasal and interorbital septa. These elements play an important role in the rigidity of the skull for their function is analogous to that of the vertical component of an I-shaped girder.

In the skulls of many birds the whole of the upper mandible is hinged to the cranium, but in *C. coccothraustes* it is rigidly fixed. The suture between the frontal and nasal bones, where the hinge is usually located, is obliterated ; the nasal and the interorbital septa form what is functionally a continuous vertical wall ; and the palatines are ankylosed with the rostrum and vomer which form most of the base of that wall.

The fixity of the upper mandible also may be associated with the nature of the relationship between the cranial head of the quadrate and the surrounding structures in the otic region of the skull. The quadrate is joined to the palatine by the pterygoid and to the upper mandible by the zygoma, and owing to the immobility of the upper mandible the quadrate is held firmly by these bones. The absence of movement together with the great crushing strain imposed on the quadrate by the lower jaw has resulted in the squamosal and opisthotic facets in the otic region extending partly around and in close contact with the small squamosal and opisthotic heads of the quadrate. The extension of the area of contact between the quadrate and the cranium is functionally possible only because the quadrate is held firmly by the pterygoid and the zygoma. The increased area of contact provides a strong base for the quadrate which in its capacity as the fulcrum of the lower jaw experiences great pressures when hard food, such as fruit stones, are cracked.

The great pressures have also influenced the nature of the quadrate which is very massive. Moreover, a powerful muscle, M. Quadrato-mandibularis, originates from its orbital process, and the inclusion of the muscle as an important member of the

Adductor Group has no doubt contributed towards the massive development of this bone.

The post-orbital process of the squamosal is unusually large and this feature may be correlated with the powerful muscle, the pars medius of the M. mandibulae externus, which has a tendinous origin on it. The pars medius is inserted into the lateral surface of the processus coronoideus, but the modifications associated with this will be discussed later.

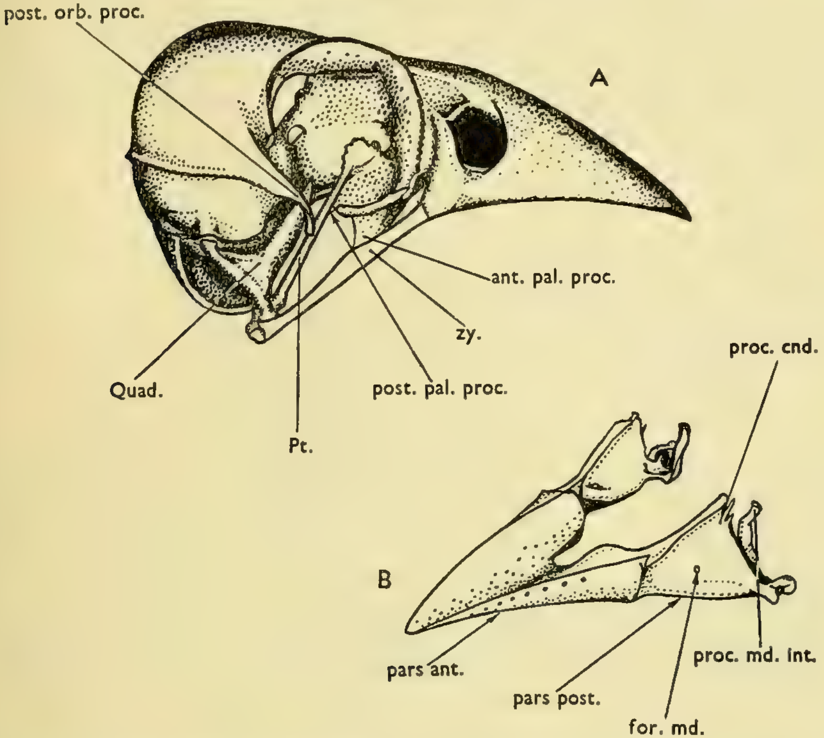

FIG. 2. ***Coccothraustes coccothraustes.*** A, cranium and upper jaw, lateral view from the right side. B, Lower jaw. *Ant. pal. proc.*, anterior process of the palatine ; *for. md.*, foramen mandibularis ; *pars. ant.*, anterior part of the lower jaw (dentary) ; *pars. post.*, posterior part of the lower jaw ; *post. orb. proc.*, post-orbital process of the squamosal ; *post. pal. proc.*, posterior process of the palatine ; *proc. cnd.*, processus coronoideus ; *proc. md. int.*, processus mandibulae internus (articular) ; *pt.*, pterygoid ; *quad.*, quadrate ; *zy.*, zygoma (quadrato-jugal and jugal).

Dislocation of the lower jaw from the quadrate during the contraction of the powerful jaw muscles is prevented by a ligament which extends from the zygoma to the posterior surface of the processus mandibulae internus, passing over the posterior surface of the distal end of the quadrate. This ligament has two centres of ossification; one forms a large sesamoid which lies close to, and posterior to, the articulation of the jaw; the other is smaller and lies more laterally near the attachment of the ligament to the zygoma.

The lower jaw, like the remainder of the skull, is massive and ossified to the extent that the foramen mandibularis, usually a large opening, is reduced to a size that permits only the passage of a branch of the trigeminal nerve (Text fig. 2*b*).

The anterior part of the lower jaw is strengthened by an inward expansion and union of the paired dentaries, the long symphysis forming a bony shelf. Posteromesially the dentaries are greatly thickened to serve as strong foundations for the heavy bosses of the rhamphotheca.

3. *Myology of the Jaw*

The muscles involved in the movement of the jaws of birds form four functional groups:

(a) The Adductor Group.
(b) The Constrictor Group.
(c) The Protractor Group.
(d) The Retractor Group.

The Adductor Group raises the lower jaw, the Constrictor Group depresses it; the Protractor Group raises the upper mandible and the Retractor Group lowers it. In *C. coccothraustes* the upper mandible is not hinged on the cranium, as already mentioned, and the muscles of the Protractor Group which persist are functionless, while the muscles of the Retractor Group assist in the elevation of the lower jaw and are dealt with here as members of the Adductor Group.

The Constrictor Group and the Protractor Group in *C. coccothraustes* each consists of only one paired muscle and therefore neither *in sensu stricto* can be considered as a "group". Nevertheless, the term has been used here for convenience in both cases.

I THE ADDUCTOR GROUP

The Adductor Group, which raises the lower jaw, is the largest of the three groups. This assemblage in *C. coccothraustes* may be further divided into two clearly marked functional units, one acting from the top and back of the cranium and the other acting from the orbital walls and their vicinity. The muscles of the former are inserted in the ramus of the lower jaw near the superior (dorsal) and the posterior margin of the coronoid elevation. Functionally, this is the more important unit and consists of the Ms. Adductor mandibulae and the M. Quadrato-mandibularis. The other muscles of the Adductor Group, the M. Pterygoideus and the M. Ethmomandibularis, are inserted near the inferior (ventral) margin of the ramus of the lower jaw.

DESCRIPTION OF THE ADDUCTOR GROUP

M. ADUCTOR MANDIBULAE EXTERNUS (Text-fig. 3)

(1) PARS SUPERFICIALIS

The rostral part is fan-like and arises from the cranium over most of the anterior half of the frontal. The area of attachment is confined anteriorally and mesially by the frontal crest, and laterally by the flattened rim of the orbit. The fibres pass forwards and downwards between the post-orbital process of the squamosal and the rim of the orbit. The fibres converge becoming more tendinous and are inserted at the apex of the processus coronoideus of the lower jaw. The main part extends over the posterior half of the frontal; it is bounded by the rostral part in front and the transverse post-frontal crest behind, and extends inwards to the meso-frontal crest. The converging fibres are directed more forwards than those of the previous part and pass over its aponeurosis and the post-orbital process of the squamosal. The head is inserted in the pars posterior of the lower jaw laterally to the head of the rostral part at the apex of the processus coronoideus. The caudal part arises from that area of the cranium bounded by the transverse post-frontal crest in front and the transverse crest on the posterior part of the squamosal and the parietal. (Mesially the two prominences converge and form a triangular area of attachment). The fibres passing more forwards than downwards become more tendinous as they converge; they are inserted somewhat laterally in the posterior margin of the processus coronoideus. This part is similar in size to

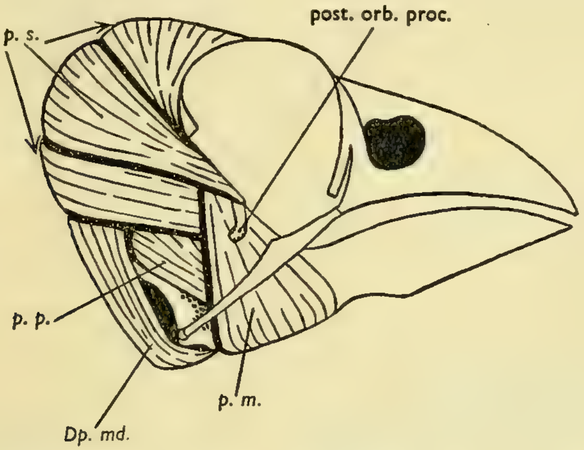

FIG. 3. ***Coccothraustes coccothraustes.*** Diagrammatic view of the right side of the head showing the external jaw muscles. *p.m.*, *p.p.*, *p.s.*, partes medius, profundus, superficialis of the M. Adductor mandibulae externus; *Dp. md.*, M. Depressor mandibulae.

the other two but it differs in that the converging fibres pass under both the distal part of the post-orbital process of the squamosal and the ascending fibres of the pars medius (see below).

(2) Pars profunda

The pars profunda arises from the cranium on the anterior surface of the supra-meatal ridge of the squamosal and in the concavity in the otic region between the cranium and the quadrate, also to the neck of the quadrate. This muscle is very tendinous throughout although it is inclined to be more fleshy in the part occupying the concavity in the otic region. It is inserted in the ramus of the lower jaw ventrally to the site of insertion of the pars superficialis, that is, about half-way along the outer edge of the posterior margin of the processus coronoideus. Some of the fibres and the dense fascia surrounding the muscle coalesce with those of the pars superficialis.

(3) Pars medius

The pars medius is a fan-like muscle with a tendinous origin on the ventral surface of the post-orbital process of the squamosal. The fibres pass downwards and become more fleshy as they diverge. The muscle is inserted over most of the lateral surface of the processus coronoideus of the lower jaw.

M. ADDUCTOR MANDIBULAE POSTERIOR (Text-fig. 4)

The M. adductor mandibulae posterior arises from the posterior wall of the orbit, namely, from the alisphenoid outside the latero-ventral margin of the fossa in the orbital wall. Mesially there is a thin bony partition which separates the muscle from the M. Pseudotemporalis (see below), and laterally another thin bony prominence extends down from the rim of the orbit and separates the muscle from the descending fibres of the pars superficialis. The muscle is short and very tendinous. It is inserted in the mesial surface of the processus coronoideus near the upper half of the posterior margin. There are a few tough ligamentous strands extending the whole length of the muscle and these are inserted in the small dorsally directed conical process of the mesial surface of the processus coronoideus near the posterior margin.

M. ADDUCTOR MANDIBULAE INTERNUS (M. PSEUDOTEMPORALIS) (Text-fig. 4)

The M. Pseudotemporalis arises on the posterior wall of the orbit from the alisphenoid below the fossa in the orbital wall. The site of attachment is separated laterally from the M. Adductor mandibulae posterior by a thin bony partition (see below), and mesially from the optic foramen by a similar partition. The muscle is tendinous throughout and it is attached to the ramus of the lower jaw in the mesial surface of the processus coronoideus. The site of attachment is a little below the antero-dorsal margin of the ramus anterior to the M. Adductor mandibulae posterior.

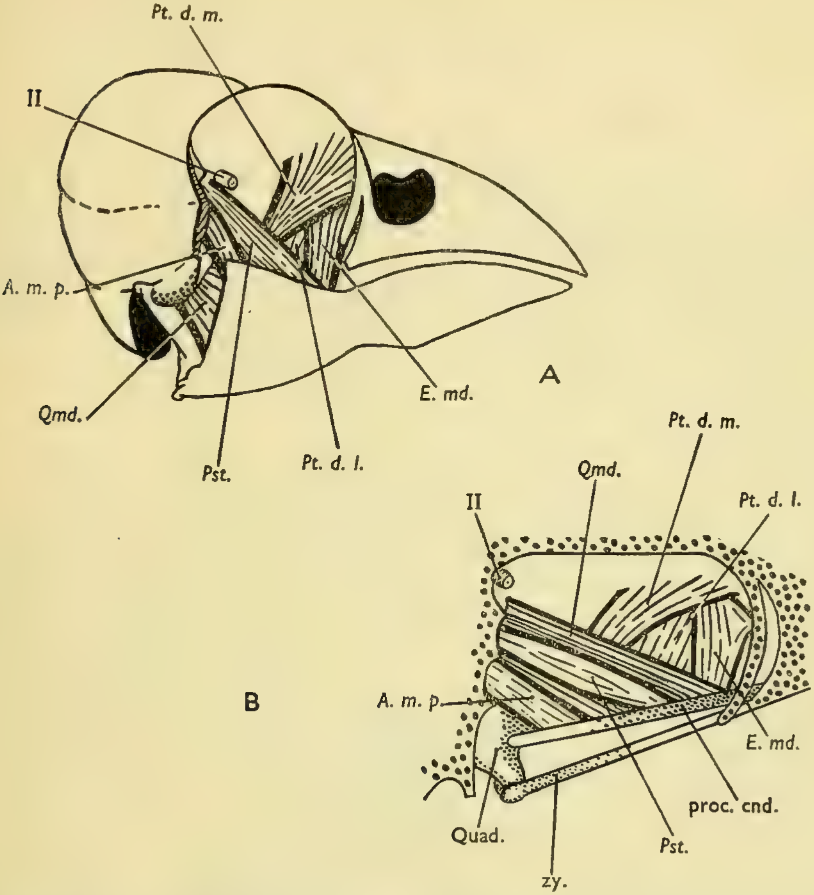

Fig. 4. ***Coccothraustes coccothraustes.*** A, Diagrammatic view of the right side of the head, eye and eye muscles removed to expose the jaw muscles in the orbit. B, Diagrammatic dorsal view of the right orbit. *A.m.p.*, M. Adductor mandibulae posterior; *E. md.*, M. Ethmo-mandibularis; *Pst.*, M. Pseudotemporalis (M. Adductor mandibulae internus); *Pt.d.l.*, M. Pterygoideus dorsalis lateralis; *Pt.d.m.*, M. Pterygoideus dorsalis medialis; *Qmd.*, M. Quadrato-mandibularis; *II*, Optic nerve.

M. QUADRATO-MANDIBULARIS (Text-fig. 4)

The M. Quadrato-mandibularis forms a thin sheet of muscle, almost devoid of tendinous tissue, underlying the Ms. Pseudotemporalis and Adductor mandibulae posterior. It extends from the quadrate to the mesial surface of the processus coronoideus. The muscle arises from both surfaces of the orbital process and as far as the neck of the quadrate where part of the pars profunda of the M. Adductor mandibulae externus originates. The muscle is inserted obliquely in the ramus of the lower jaw along a line tending to pass from below the site of insertion of the M. Pseudotemporalis towards the point of articulation with the quadrate.

M. ETHMO-MANDIBULARIS (Text-fig. 5)

The M. Ethmo-mandibularis arises from the anterior part of the interorbital septum above the palatine and partly from the anterior wall of the orbit, that is, from the mesethmoid. Some of the dorsal fibres pass horizontally across the anterior angle of the orbit and assist in the support of the main fibres which pass obliquely downwards and outwards back to that part of the lower jaw behind the gape. The fibres become tendinous a little before being inserted into the mesial surface of the ramus of the lower jaw above the ventral margin.

M. PTERYGOIDEUS (Text-fig. 5)

M. PTERYGOIDEUS DORSALIS

M. Pterygoideus dorsalis medialis

The M. Pterygoideus dorsalis medialis arises from the interorbital septum at the antero-dorsal angle of the orbital wall above the attachment of the posterior part of the M. Ethmo-mandibularis. The muscle has numerous tendinous fibres near its site of origin, and these increase in number until the muscle is completely tendinous a little before the site of insertion. The muscle passes backwards and downwards between the ventral surface of the orbital process of the quadrate and the dorsal surface of the pterygoid (beneath the M. Protractor pterygoidei, see below). The muscle is attached by a very strong tendon to the ramus of the lower jaw at the head of the processus mandibulae internus. The tendon lies over the head of the inflexion and is inserted into the upper part of the posterior surface.

M. Pterygoideus dorsalis lateralis

The M. Pterygoideus dorsalis lateralis arises principally from the palatine and from the flattened area at the union of the pterygoid and the palatine. The thick fleshy fibres pass obliquely downwards and backwards and outwards to the site of insertion which is towards the ventral margin of the mesial surface of the ramus of the lower jaw, posterior to the M. Ethmo-mandibularis. The only tendinous tissue in the muscle is in the nature of a thin sheet extending throughout the entire muscle.

M. PTERYGOIDEUS VENTRALIS

M. Pterygoideus ventralis medialis

The M. Pterygoideus ventralis medialis arises from near the top of the mesial surface of the processus mandibulae internus. It is a slender muscle and the fibres pass forwards and upwards becoming more tendinous. The tendon is inserted in the palatine along the outer (ventral) surface of the posterior process where it curves as if to meet the other member of the pair.

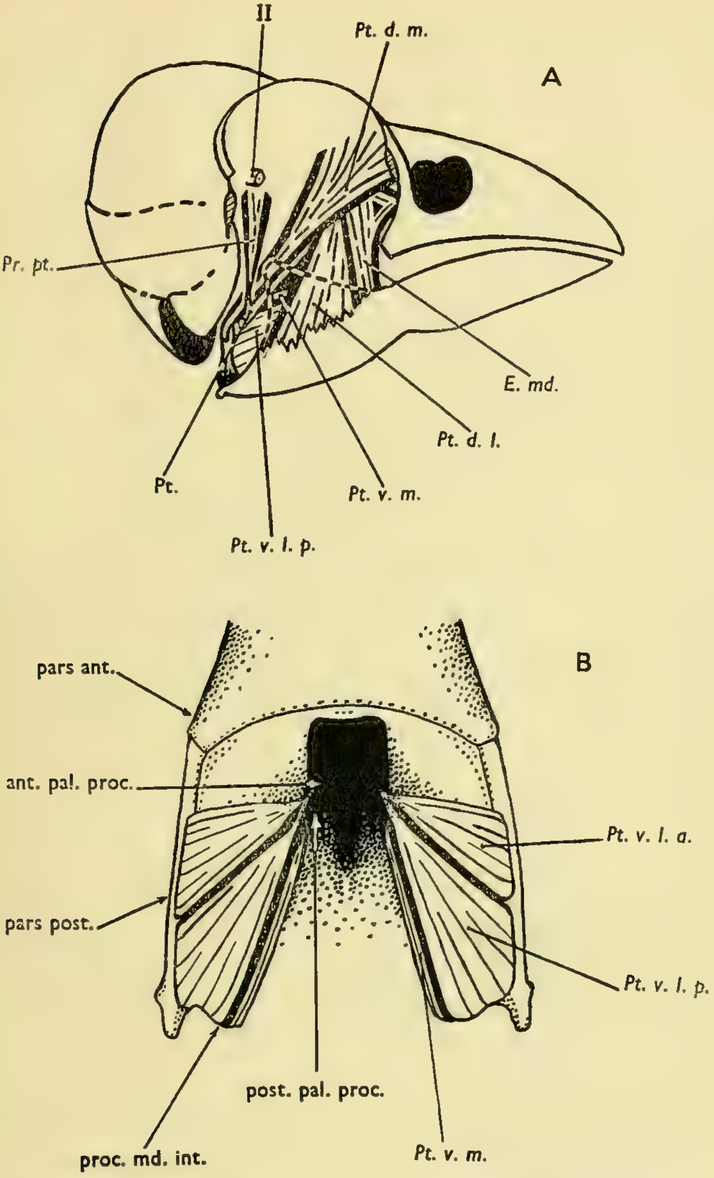
II
Pt. d. m.
A
Pr. pt.
E. md.
Pt. d. l.
Pt.
Pt. v. m.
Pt. v. l. p.
B
pars ant.
ant. pal. proc.
Pt. v. l. a.
pars post.
Pt. v. l. p.
post. pal. proc.
proc. md. int.
Pt. v. m.

Fig. 5. ***Coccothraustes coccothraustes.*** A, Diagrammatic view of the right side of the head dissected to expose the ventral jaw muscles. B, Diagrammatic ventral view of the ventral jaw muscles. *Pr.pt.*, M. Protractor pterygoidei ; *Pt.v.l.a.*, anterior portion of the M. Pterygoideus ventralis lateralis ; *Pt.v.l.p.*, posterior portion of the M. Ptergoideus ventralis lateralis ; *Pt.v.m.*, M. Pterygoideus ventralis medialis.

M. Pterygoideus ventralis lateralis

Anterior Portion. The anterior portion of the M. Pterygoideus ventralis lateralis is a thin fan-like muscle arising mainly from the ventral margin and partly from the mesial surface of the ramus of the lower jaw. The site of attachment is mid-way along the ventral margin of the pars posterior of the ramus. The fibres pass upwards mesially to other muscles, then they become more tendinous and are inserted along the outer member of the bifurcation at the distal end of the anterior palatine process.

Posterior Portion. The posterior portion of the M. Pterygoideus ventralis lateralis is a stouter muscle than the anterior portion. It arises along most of the mesial surface of the processus mandibulae internus of the lower jaw, that is, all of the mesial surface except for the small area occupied by the M. Pterygoideus ventralis medialis. It is also attached along a little of the ventral margin and mesial surface of the main body of the ramus of the lower jaw. The fibres are markedly tendinous and ultimately form a tough tendon which in inserted along the inner branch of the bifurcation at the distal end of the anterior palatine process (the anterior portion is attached to the outer branch).

Remarks on the Adductor Group

The relatively large area of attachment of the muscles of the Adductor Group indicates that the total stress of the combined contraction is evenly distributed over most of the cranium. The M. Adductor mandibulae externus arises over the lateral, dorsal, and posterior surfaces of the cranium and the Ms. Adductor mandibulae posterior and internus (M. Pseudotemporalis) arise over the anterior of the cranium, that is, the posterior wall of the orbit. The Ms. Pterygoideus and Ethmo-mandibularis are attached to the mesethmoid, palatine and the pterygoid and the stress of their contraction is relayed to the antero-ventral surface of the cranium by the interorbital septum.

Functionally, it is not strictly correct to include all the elements of the M. Pterygoideus in the Adductor Group of muscles, for when both the mesial members of the M. Pterygoideus dorsalis and ventralis contract they seem to assist in the depression of the lower jaw ; they draw the processus mandibulae internus of the articular forwards, and so rotate the anterior of the lower jaw downwards through the same angle (Text fig. 6). However, on closer examination it becomes apparent that these muscles and the posterior portion of the M. Pterygoideus ventralis lateralis hold the articulatory surfaces of the lower jaw and the quadrate in contact. Thus they strengthen the hinge mechanism and help prevent the dislocation of the jaw when the powerful crushing muscles contract.

If the upper mandible of *C. coccothraustes* were hinged and the palatines were free and formed part of this mechanism then those members of the Ms. Pterygoideus dorsalis and ventralis which are inserted in the palatines would act as *retractor* muscles. These would draw the palatines backwards so lowering the upper mandible and holding it fast. However, it seems proper to include all the members of the Ms. Pterygoideus dorsalis and ventralis in the Adductor Group for by their contractions they ensure the most efficient functioning of the main " adducting " muscles.

Not only is it valid to include these muscles in the same functional group because of their necessary simultaneous contractions but because they are innervated by the same branch of the trigeminal nerve.

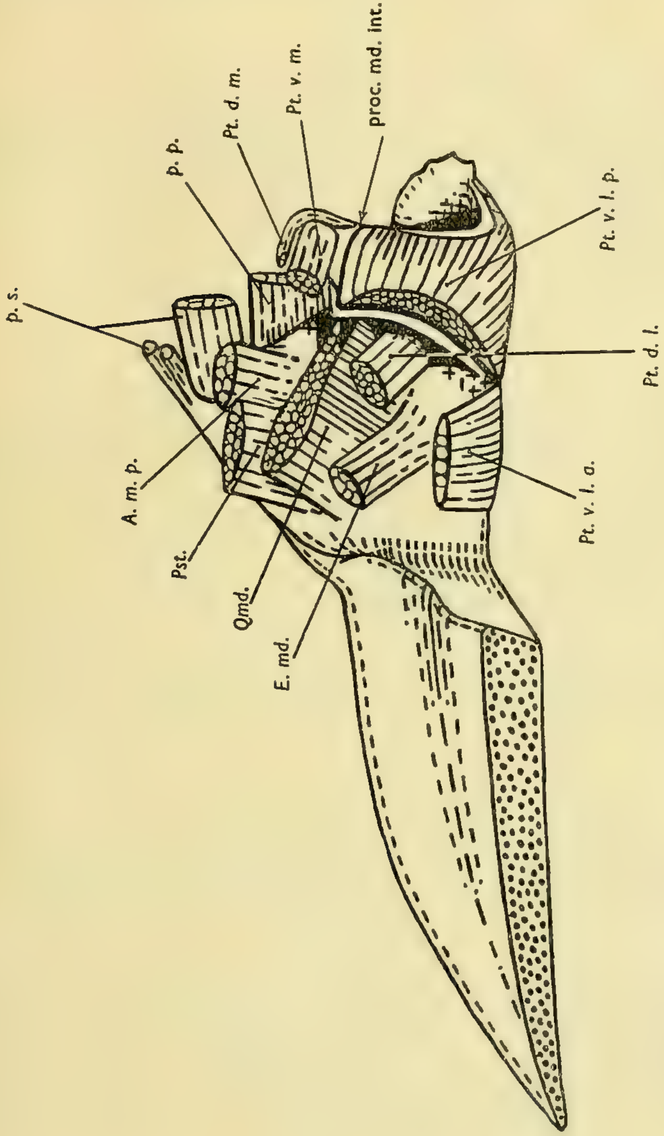
p. s.
A. m. p.
Pst.
Qmd.
E. md.
p. p.
Pt. d. m.
Pt. v. m.
proc. md. int.
Pt. v. l. p.
Pt. d. l.
Pt. v. l. a.

FIG. 6. ***Coccothraustes coccothraustes.*** Diagrammatic view from the left of the right sagittal half of the lower jaw showing the sites of origin or insertion of the jaw muscles over the mesial surface.

II THE CONSTRICTOR "GROUP"

The depression of the lower jaw, as mentioned above, is effected by only one paired muscle.

DESCRIPTION OF THE CONSTRICTOR "GROUP"

M. DEPRESSOR MANDIBULAE (Text-figs. 3 and 7)

The M. Depressor mandibulae arises from the greater part of the exoccipital, especially the part forming the posterior wall of the bony meatus. The fibres of the muscle pass downwards without converging, or becoming very tendinous, to where they are inserted into the post-articular part of the mandible. Tendinous insertions are made in the angular behind the lateral process, ventrally in the posterior of the angular, and in the posterior of the processus mandibulae internus. The fibres form a flat muscle which completely covers the mandibular articulation from behind and also forms a fleshy extension to the posterior wall of the meatus.

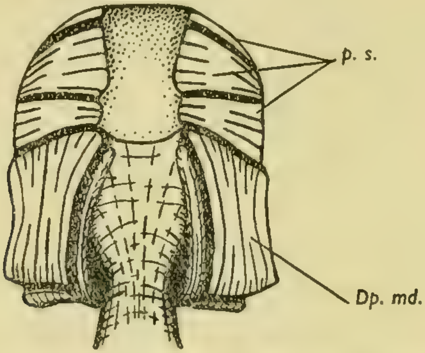

FIG. 7. ***Coccothraustes coccothraustes.*** Diagrammatic posterior view of the head showing the external jaw muscles.

REMARKS ON THE CONSTRICTOR "GROUP"

The M. Depressor mandibulae is a feeble muscle in comparison with the muscles of the Adductor Group. Its action does not necessitate any rapid contraction, nor is it required to exert any great force to depress the lower jaw. The chief function of the muscle is to overcome the effect of the relaxed, but unextended, muscles of the Adductor Group that would otherwise tend to oppose the depression of the lower jaw.

III THE PROTRACTOR "GROUP"

The upper mandible does not articulate on the cranium in *C. coccothraustes* but although this mechanism is absent one functionless paired muscle, as already mentioned, persists as a vestigial structure.

DESCRIPTION OF THE PROTRACTOR "GROUP"

M. PROTRACTOR PTERYGOIDEI (Text-fig. 5)

The M. Protractor pterygoidei is a slender muscle arising from the alisphenoid in the posterior wall of the orbit a little below the optic foramen. The fibres pass downwards and outwards beneath the orbital process of the quadrate ; they converge and becoming tendinous are attached to a small dorsally situated spine-like process near the quadratal end of the pterygoid.

REMARKS ON THE PROTRACTOR "GROUP"

In species where the upper mandible is hinged on the cranium the function of the M. Protractor pterygoidei is to draw the distal (quadratal) end of the pterygoid upwards. The quadrate is attached to this and when the pterygoid moves upwards the quadrate is rotated forward, thrusting the pterygoid forward at the same time. This action pushes forward the palatine under the interorbital septum. The upper mandible is hinged to the cranium on the dorsal side so that forward movement on the ventral side communicated by the palatines has the effect of lifting the bill on its hinge. The zygoma is also attached to the quadrate and the forward rotation of the quadrate causes the zygoma to be moved forward, thus assisting in the elevation of the upper mandible since the zygoma is joined to the maxilla. Although the muscle is functionless in *C. coccothraustes* is is interesting to note that its fibres are not completely lacking in tendinous strands and generally the muscle closely resembles the form of the muscles of the Adductor Group.

COMPARATIVE NOTE

For comparative purposes the Chaffinch, *Fringilla coelebs*, and the Brambling, *F. montifringilla*, have been selected as more generalized fringilline species.

In comparison with *C. coccothraustes* the oral surfaces of the rhamphotheca of *F. coelebs* are smooth and lack any dilations similar to the striated pads, or bosses (Text-fig. 8*b*). It would appear (Sushkin, 1925) that this specialization is not confined to *C. coccothraustes* for apart from *Hesperiphona* of North America the occurrence of specializations of this nature are found in a few other Old World genera, namely, *Eophona*, *Perissospiza* and *Mycerobas*.

In comparison with the skull of *C. coccothraustes* that of *F. coelebs* is a fragile structure and this difference is illustrated by comparing the sizes and the weights of the skulls of the two species. The average maximum dimensions of skulls of *C. coccothraustes* are 40 × 20 × 20 mm. and *F. coelebs* 30 × 14 × 15 mm.; if the cube of each of the linear proportions of the skull of *C. coccothraustes* is compared with those of a hypothetical skull of the same average dimensions as *F. coelebs*, but of the *same design* as that of *C. coccothraustes*, it is found that the dimensions of the skull of *C. coccothraustes* average 250% " larger ". Yet the average weights of the skulls of *C. coccothraustes* and *F. coelebs* are 3·235 gm. and 0·654 gm. respectively, that is, the skull of *C. coccothraustes* contains nearly 400% more bony material than that of *F. coelebs*. Therefore, the skull of *C. coccothraustes* is very massive for its size.

The outline of the skull of *C. coccothraustes* has been likened to one horn of a crescent, but the skull of *F. coelebs* differs by being more cuneiform, and its dorsal profile is nearly straight (Text-fig. 8*a*). The difference is attributable mainly to the greater angle between the basi-cranial and basi-maxillary axes[1] in *F. coelebs* which is 150° but only 120° in *C. coccothraustes*.

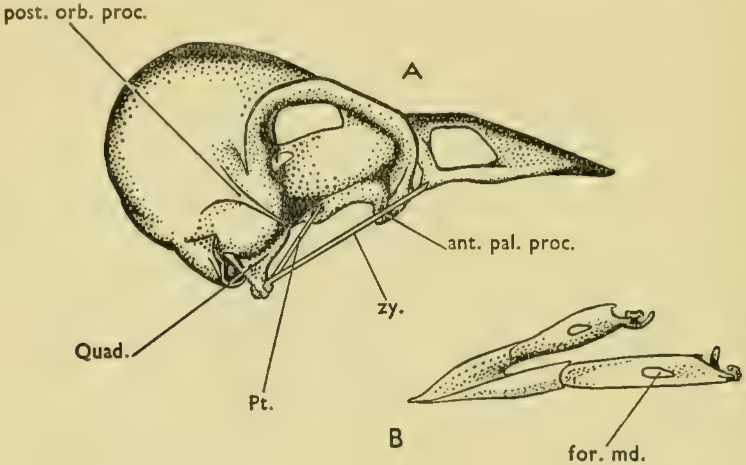

FIG. 8. ***Fringilla coelebs.*** A, Cranium and upper jaw lateral view from the right side (compare Text-fig. 2*a*). B, Lower jaw (compare Text-fig. 2*b*).

Van der Klaauw and Duijm consider that a difference of this nature can be a functional adaptation and Duijm stated, " . . . the bill and the cerebral capsule behave mainly as independent functional elements.". In the present instance the downward rotation of the bill relative to the cranium in *C. coccothraustes* reduces some of the stresses set up by the application of powerful forces to crack fruit stones. This is shown diagrammatically in fig. 9. Here BC and AB represent the basi-maxillary axis and a line parallel to the basi-cranial axis in two skulls of the same overall length. In (A) the subtended angle between the two is 120° as in *C. cocco-*

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[1] Basi-maxillary axis: The line of intersection between the vertical longitudinal plane of the head and the mean ventral surface of the premaxillae.

thraustes, and in (B) it is 150° as in *F. coelebs*. Assuming that the same forces were applied to the lower jaw to crack a nut held at the same distance from the angle of the jaw, then the magnitude and direction of the force, relative to the upper jaw, can be represented as the line XY. The direction of the force is tangential to a circle whose centre is at the articulation of the lower jaw, A, and periphery at D, where the lower mandible presses against the stone. The force XY is resolvable into two components at right angles to one another, XP and XQ. The former exerts a compressional and the latter a bending strain on the upper jaw. A bending strain is clearly more likely to fracture the bill than a compressional strain along its length and the bending component is approximately 6% less in (A) where the angle between bill and cranium is similar to that of *C. coccothraustes*. Therefore, the downward rotation of the bill in *C. coccothraustes* may be regarded as an adaptation to feeding so that hard stones are cracked with a smaller bending strain being experienced by the bill; that is, there is less chance of fracture than in a skull of the design of *F. coelebs* where the subtended angle between the bill and cranium is more obtuse.

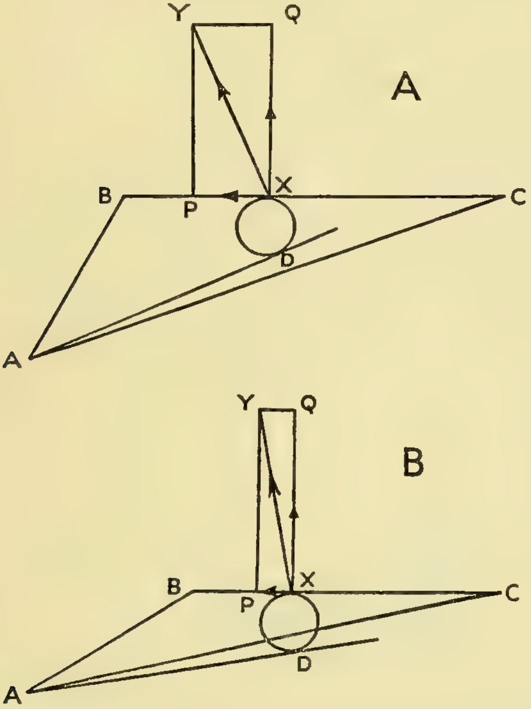

FIG. 9. Diagram showing the main forces imposed on the upper jaw when food is crushed between the mandibles. A, The subtended angle, ABC, between the basi-maxillary and basi-cranial axes is 120°. B, The subtended angle is 150°.

The bending strain which is experienced by the bill of *C. coccothraustes* when fruit stones are cracked must nevertheless still be relatively enormous when forces in the region of 100 lb. have to be applied to crack them, but its effect is largely nullified by the highly ossified septa. These are markedly different in *F. coelebs* where the interorbital septum exhibits a more normal passerine condition forming only a thin bony partition between the orbits and the nasal septum appears to be mainly unossified.

Again, a high degree of ossification is found in the pterygoid-quadrate-zygoma system, for in comparison the pterygoids and zygomae of *F. coelebs* are long and slender, while the quadrates of *C. coccothraustes* are about twice the size of those of *F. coelebs*.[1]

An examination of the skulls reveals that not only has the skull of *C. coccothraustes* become modified to withstand greater stress, but also to provide a greater area of the attachment and insertion of the jaw muscles. This latter point is well illustrated by the difference observed between the lower jaw of *C. coccothraustes* and *F. coelebs*. In the former the coronoid is elevated in correlation with the large size of the pars medius of the M. Adductor mandibulae externus which is inserted into it, moreover, the foramen mandibularis is very small while it is relatively large in *F. coelebs* (Text-fig. 10). The disparity in the sizes of the partes medii in the two birds is also reflected in the degree of development of the respective post-orbital processes of the squamosals from which they originate. Generally the lower jaw of *F. coelebs* appears to be more primitive in character than that of *C. coccothraustes* which, in addition to the adaptations just referred to, is modified to carry the heavy bosses of the bill, as described above.

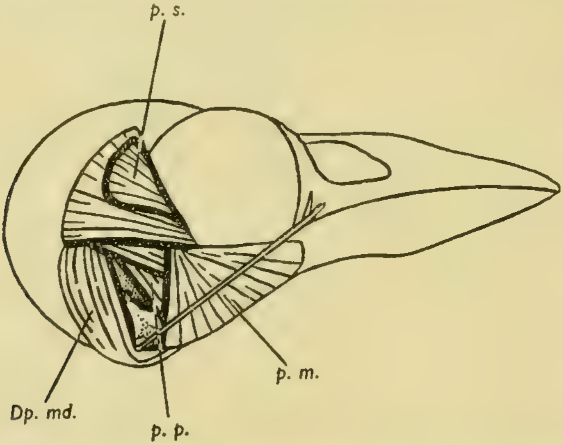

FIG. 10. ***Fringilla montifringilla.*** Diagrammatic view of the right side of the head showing the external jaw muscles (compare Text-fig. 3).

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[1] Quadrate of *C. coccothraustes :* mass 0·0375 gm., 9 mm. high × 7 mm. long (orb. proc.). Quadrate of *F. coelebs :* mass 0·0041 gm., 4·5 mm. high × 4·5 mm (orb. proc.).

The jaw muscles of *C. coccothraustes* in comparison with those of the Brambling, *Fringilla montifringilla*, are exceedingly tendinous. In the latter they are composed of fleshy fibres almost devoid of tendons, except at the site of insertion, and even then the tendons are not as evident as those in *C. coccothraustes*. The jaw muscles of *F. montifringilla* are generally more bulky and appear to contain much non-contractile tissue. One gains the impression that the flaccid muscles of *F. montifringilla* are incapable of the rapid powerful contractions of the muscles of *C. coccothraustes*.

The difference in the form of the M. Adductor mandibulae internus (M. Pseudotemporalis) in the two species illustrates the comparatively compact nature of the muscles of *C. coccothraustes*. In this bird the M. pseudotemporalis is squarish in cross-section and extends from the posterior wall of the orbit to the lower jaw. In *F. montifringilla*, on the other hand, the M. pseudotemporalis although similarly attached and inserted forms a fleshy floor to the orbit filling the spaces between the Ms. Adductor mandibulae posterior, Pterygoideus dorsalis and Ethmo-mandibularis. Yet, despite its size, the muscle probably does not contract with the same forces as its smaller counterpart in *C. coccothraustes*.

The nature of the jaw muscles in *C. coccothraustes* is not the only factor contributing to a powerful musculature, but their size and distribution are also important. A comparison of the relative sizes and the areas of attachment of the various portions of the M. Adductor mandibular externus illustrates this point. It can be seen (Text-figs. 3 and 10) that the area of attachment of this muscle in *C. coccothraustes* is disproportionately greater than in *F. montifringila*. In *C. coccothraustes* the muscle arises from over most of the external surface of the cranium whereas in *F. montifringilla* the areas of attachment are confined to the lateral and postero-lateral surfaces.

The essential difference between the myology of the jaw of *C. coccothraustes* and that of *F. montifringilla* appears to be one of degree, that is, area of attachment and tendinosity. However, what I have termed the " anterior portion " of the M. Pterygoideus ventralis lateralis appears to be absent in *F. montifringilla*. In this species the M. Ethmo-mandibularis is more prominent and its site of origin extends over the comparable area of origin of the anterior portion of the M. Pterygoideus ventralis lateralis in *C. coccothraustes*. It would appear from this that the M. Ethmo-mandibularis is divided into two parts in *C. coccothraustes*. However, since in *C. coccothraustes* the anterior portion is inserted into the palatine along with the posterior portion of the M. Pterygoideus ventralis lateralis I am of the opinion that the anterior portion should be considered as a part of the M. Pterygoideus ventralis lateralis, and this seems justifiable since the portions are also functionally complementary.

DISCUSSION

The purpose of this paper has been to indicate some of the modifications in the morphology of the head of *C. coccothraustes* which appear to be related to its ability to crack open various fruit stones, such as those of the cherry, damson and olive. There are, however, several points requiring further investigation.

There is, for example, a point of interest in the development of the horny pads of the rhamphotheca. It seems that these pads, or bosses, do not appear until the bird reaches maturity. In the limited sample examined they were not found in nestlings nor in birds in immature plumage. Even if pads were present in young birds they would be non-functional because from an examination of the stomach contents it appears that the adults are primarily insectivorous during the breeding season (Mountfort, in press) which indicates that the nestlings are fed mainly on insects. Similarly, the pads are not required by immature birds because they have been observed to feed on caterpillars, especially the Hornbeam caterpillar, *Carpinus betulus.*

The appearance of the horny pads late in the development of the individual could be interpreted as evidence that the structures have been acquired recently in the history of the species. However attractive this argument may appear to be at first sight it is misleading because the pads should not be considered apart from the associated osteological and myological modifications ; and it is possible that if the pads were present in an immature bird they would even be a danger to it ! One of the chief characteristics of young passerine birds is the absence of osseous material in most of the cranium and the slow rate at which ossification occurs as the young bird matures. The absence of osseous material makes the skull extremely fragile, the more so since the sutures between the bones remain open almost until maturity. The skull of a young bird is, therefore, not strong enough either to wishstand the stresses of cracking open fruit-stone kernals or to accomodate the powerful musculature capable of closing the jaws with a force in the region of 100 pounds, that is if the muscles could be precociously developed to contract with that force. It seems, therefore, that the late development of the pads cannot be regarded as indicative of their appearance in the phylogeny of the bird.

CONCLUSIONS

The structural modifications which have occurred in the head of *C. coccothraustes* and enable the bird to apply and withstand a force in the region of 100 lb. are profound. It appears that no part of the head, which has been considered, has escaped specialization. The oral surfaces of the horny bill are modified and equipped with striated pads between which the food is gripped. The skull, particularly the upper and lower mandibles, is strengthened to withstand the stress of cracking a hard fruit stone and it is modified to accommodate the powerful musculature of the jaw as well as to withstand the force of the contraction of the muscles. The musculature of the head is highly developed with large areas of attachment, and the individual muscles are tendinous in nature and powerful in action.

The possession of these modifications are undoubtedly a selective advantage to the bird particularly during the period of great increases in population which partly coincides with the " soft-fruit " season. *C. coccothraustes* comes less into competition with other seed-eaters and its own young at an important time of the year by utilizing fruit-stones and similar large seeds, berries and, during the breeding season, large insects.

APPENDIX

Crushing Tests on Cherry and Olive Stones

(*a*) The National Physical Laboratory carried out a series of crushing tests and made the following report:

The apparatus used for the tests was designed to simulate, as far as possible, the mandibles and pressure pads of this bird. It consisted of a steel compression rig with two ¼-in. diameter rods which fitted into two deep grooves in the lower block of the apparatus, and a flat serrated cross piece attached to the upper block. The bare fruit stone was placed between these loading points and cracked; the load being increased by moving a jockey weight along the lever of the testing machine. The time taken to crack each stone was approximately 20 seconds.

In order to represent the influence of the direction of the seam or suture of the stone in the bird's beak, the tests were made with the seam facing several directions.

The results of the tests are given in Tables I and II.

(*b*) Mr. D. B. Welbourne, of the Department of Engineering, Cambridge, working independently obtained comparable values when he crushed cherry stones in a Housefield Tensometer. In correspondence, he writes, that in his tests he effected different rates of loading and found that more rapid loading resulted in higher failure loads, that is, a greater pressure is required to break a stone quickly than to break it slowly. Therefore, the crushing loads given in Tables I and II should not be regarded as the maximum pressures applied by *C. coccothraustes* when cracking fruit stones; for the values, determined by the tests, were obtained in each case by applying the pressure for approximately 20 sec. which is a greater time than it takes *C. coccothraustes* to crack a fruit stone.

TABLE I.—*Crushing tests on Cherry Stones*

Test	*Direction of seam*	*Type of Cherry*	*Crushing load (lb.)*
1	Sideways	Dark	64
2	,,	,,	62
3	,,	,,	70
4	,,	,,	62
5	Upwards	,,	70
6	,,	,,	65
7	Downwards	,,	61
8	,,	,,	60
9	,,	,,	62
10	,,	,,	65
1	Sideways	Light	95
2	,,	,,	93
3	Upwards	,,	70
4	,,	,,	68
5	,,	,,	70

TABLE II.—*Crushing tests on fresh Olive Stones*

Test	*Direction of seam*	*Type of stone*	*Crushing load* (lb.)
1	Sideways	Olive	111
2	,,	,,	110
3	,,	,,	106
4	,,	,,	114
5	Upwards	,,	125
6	,,	,,	137
7	,,	,,	147
8	,,	,,	143
9	Downwards	,,	136
10	,,	,,	107
11	,,	,,	138
12	,,	,,	159

Physic's Division.
National Physical Laboratory.

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